THE ROLE OF HABITAT STRUCTURAL GRADIENTS ON THE DISTRIBUTION OF SMALL RODENTS IN THE SOUTH BRAZILIAN RESTINGA (MAMMALIA, RODENTIA, CRICETIDAE).

DISSERTATION

zur Erlangung des akademischen Grades eines

Doktors der Philosophie

der Philosophischen Fakultät

der Universität des Saarlandes

von

LUIZ FLAMARION BARBOSA DE OLIVEIRA

Saarbrücken

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By

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Rio Grande do Sul, Brazil

Submitted to the Graduate Faculty of Philosophy
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy.

UNIVERSITY OF SAARLAND
1990

Gedruckt mit Unterstützung des Deutschen Akademischen
Austauschdienstes (DAAD)

Der Dekan: Prof.Lic.Dr. Gert Hummel

Berichterstatter: Prof.Dr.Dr.h.c. Paul Müller
Priv.Doz.Dr. Peter Nagel

Tag der letzten Prüfungsleistung: 13.August.1990

FOREWARD

I am sincerely grateful to Prof. Dr. Paul Müller for his invitation and for providing an opportunity for execute this work at the Institute of Biogeography.

I am deeply indebted to Prof. Dr. Margarete S. Mattevi (Universidade Federal do Rio Grande do Sul) for her help and encouragement throughout the course of this study.

I particularly acknowledge T.R.O. Freitas for his assistance in several stages of this work.

For the help and advice in computing my data related to CCA analysis, I am indebted to Dr. C.J.F. Ter Braak (TNO Institute of Applied Computer Science, Wageningen).

I thank the SEMA (Secretaria Especial do Meio Ambiente) for permission and logistic support for working at Estaçao Ecológica do Taim.

I thank Dr. M. Lock (Museu Nacional, Rio de Janeiro) for her assistance in making available for examination specimens of rodents housed under her supervision.

I am grateful to Clemente Daitx and to the Mayes families for permission to work on their property and for the kindness they extended to me during the field work in Faxinal (Torres) and in Santa Catarina Island, respectively.

I thank N. Zanchin, B. Castro, A.U. Christoff and L.L. da Silva for assistance in collecting the rodent species in some of the studied areas.

I am indebted to Prof. Dr. I.D. Pinto (CECLIMAR - Centro de Estudos Costeiros Limnológicos e Marinhos - UFRGS) for logistic help and laboratory facilities at the CECLIMAR, in different stages of the work in the north of the Coastal Plain.

Special thanks go to Dr. A. Janssen (Universität des Saarlandes) for her friendly words and encouragement.

Among others that have assisted me with this work I gratefully acknowledge J.L. Waechter (UFRGS), H. Hasenack (UFRGS) and W.A. Voss (Fundaçao Zoobotânica do Estado do Rio Grande do Sul) for their encouragement.

I thank Dr. A. Lall (Sch. of Entomology, St. John's College, Agra, India) for reading and correcting the English manuscript.

I acknowledge support from DAAD (Deutscher Akademischer Austauschdienst) for this study.

The field work was supported in part by the grant no. 408780/85 from the Brazilian Research Council - CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico).

I express my gratitude to Elaine for suggestions and spiritual uplifting.

ABSTRACT

The Restinga regions in southern Brazil (Quaternary coastal plains) are characterized by a vegetational complex. The vegetation ranges from almost naked dunes, grassy swamps to woodlands and closed forests. Several vegetation zones contrast strongly and the drain conditions may perform a central role in different habitat types.

The evaluation performed in seventeen areas along the Coastal Plain, and in the south-brazilian highland slopes in Rio Grande do Sul and in the Santa Catarina Island, demonstrated that the rodent fauna is differently composed particularly along the coast. The species composition varies markedly from North to South and West to East. The assemblages on the northern portion of the coast in Rio Grande do Sul and in the Santa Catarina Island showed high similarity to those found in the south-brazilian highland slopes. Thus the changes in the rodent fauna composition do not coincide with abrupt changes in the topographic features. The northern Restinga assemblages are more tropical and forest elements are common. The southern and central rodent assemblages present high similarity with the Uruguayan and eastern Argentina fauna and several species are closely associated to grasslands. None of the cricetid species found is endemic to the Restinga, since all of them occur in neighbouring areas and several are largely distributed in other regions of South America.

In four regions the classification of trap sites based on sample scores that are derived from the species scores and from the linear combination of structural environmental variables by the Canonical Correspondence

Analysis (CCA) was used to assess the species environment relationships.

The assessment of habitat components effect on rodent distribution was evaluated by Partial Canonical Correspondence Analysis and the significance of the ordinations were tested by the Monte Carlo permutation test.

The rodent assemblages' characteristics were normally determined by the habitat features. The species were mainly affected by patch structure and availability of sites with high ground cover and foliage height density. Only in sites virtually free of the livestock grazing effects the rodent assemblages approximate to the original composition.

For one sampling site a multiple-regression procedure was used to estimate the relative independent effect of species interactions and habitat structure on habitat use by each species. A community matrix that estimates the species interactions coefficients between species pairs was generated. The results give strong support to the hypothesis that the microhabitat structure determines the rodent assemblage features and that mutual inhibitory relationships between species are not important. The results show that the prediction of the assemblage composition and structure, within a single biogeographic unit, and in relatively small areas, can be made by the habitat features since the assemblages composition changes normally accompany changes in the habitat structure and the habitat selection appears to be the major factor to distribute species among the habitats.

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In Brazil, recent ecological studies relating small rodents and habitats features have been conducted. However, they are normally related to the tropical major formations as the savanna-like Cerrado vegetation in central (ALHO, 1981; ALHO et al., 1986; MARES et al., 1986), in the xeric Caatinga (STREILEIN, 1982) in northeastern, and in the Pantanal (LACHER et al., 1986; LACHER and ALHO, 1989), a large wetland in southwestern Brazil. Data about other formations, particularly in southern regions are rare or completely absent (OLIVEIRA, 1985).

In terrestrial communities, plants form the basic patchwork structure (THOMPSON, 1985) within which biological intractions occur. The habitats are normally patchy and differ in their structure. Thus, the pattern of habitat use results in different responses among the species by selecting among compared alternatives or by some external pressure imposing a differential distribution of individuals within patches. The habitats are complex resources and their features are important components, more often than other dimensions, on the niche of species (SCHOENER, 1974a). The evidence that species respond to structural components of their environment on a scale of resolution much finer than gross habitat differences lead to a proliferation of studies on microhabitat partition. Much effort has been devoted to understand the composition and structure of communities and the species relations with the habitat structure. Several works have centered on vertebrates, particularly birds (MacARTHUR, 1958; MacARTHUR and MacARTHUR, 1961 CYR, 1977; CODY, 1981; PRODON and LEBRETON, 1981; WINKLER and LEISLER, 1981; LEISLER and WINKLER, 1985; ROTENBERRY AND WIENS, 1980; WIENS, 1986) and small mammals (ROSENZWEIG and WINAKUR, 1969; DUESER and SHUGART, 1978, 1979; KITCHINGS and LEVY, 1981; SHARPLES, 1983; SEAGLE, 1985;

I. INTRODUCTION

The Neotropical Region constitutes the richest major biotic region of the world from the point of view of number of genera and species of mammals (KEAST, 1972). No single order is absolutely confined to the Region. However, genera and species endemisms are extremely high (HERSHKOVITZ, 1972). Twelve orders, 50 families, 278 genera and 810 species have been recorded (HERSHKOVITZ, 1972). About 52 genera and more of 250 recognized species of cricetids of the subfamily Sigmodontinae (REIG, 1980) live south of Panamá amounting by themselves to 21,9% of the species of the South American mammals (REIG, 1981, 1987). The time of arrival in South America and the possible area of adaptative radiation of the group (South, Central or North America) and divergence from the original stock are controversial (SAVAGE, 1974; BASKIN, 1978; JACOBS and LINDSAY, 1984; SLAUGHTER and UBELAKER, 1984; REIG, 1986). Nevertheless, the pattern of present distribution suggests that most of the evolution of the group occurred in the north and southern central Andes (REIG, 1984, 1986, 1987) and were closely related to the climate during Pleistocene glacial that maximum affected the distribution of savanna-grassland vegetation in the Continent (WEBB, 1978; MARSHALL, 1972). The establishment of new habitats favoured the adaptative radiation of the group leading to seven tribes (REIG, 1980, 1981) that include species with a great variety of trophic, habitat, and locomotory adaptations that occur in a large variety of habitats in the Continent.

ANGELSTAM et al, 1987; WYWIALOWSKI, 1987). In the latter group, particularly for the rodents, the habitat is the principal resource partitioned (SCHOENER, 1974; PRICE, 1978; MESERVE, 1977, 1981).

Environmental variables have been found to influence distribution of species and have been frequently incorporated into ecological studies. Nevertheless, several evidences indicate that many coexisting species of small mammals interact competitively (GRANT, 1972, 1978; BROWN, 1978; HALLET et al., 1983; FRAMSTAD and STENSETH, 1984). On the other hand, the actual pattern on habitat use among species is likely to have evolved as a result of past competition (ROSENZWEIG, 1974, 1977; PIMM and ROSENZWEIG, 1981) which makes the interaction very weak or not detectable at present. The role and ways by which population processes interact with environments and the remaining components of the communities is a basic ecological question. Such interactions determine the patterns of the geographical distribution. The temporal and spatial dynamics of rodent assemblages composition, when assessed in recent areas, allow to test the hypothesis on recent assemblages where the major forces that structure the communities may still be working. Such processes may be well analysed in the Quaternary plains near the ocean as the Restinga; a new patchwork where new habitats are formed and new assemblages may be recently structured.

The word Restinga in Brazilian linguistic usage has several meanings. Normally it is used to designate the forest types near the coasts. The term is used also to nominate all the coastal vegetation types on Holocene sandy plains and sometimes reffers to sandy landscape near the ocean and the associated vegetation (ULE, 1901; RAWITSCHER, 1944; DANSEREAU, 1947; RIZZINI, 1963, 1979; JAKOBI, 1977; WAECHTER, 1985). The Brazilian literature on

coastal environments designates Restinga as sand ridges along the coasts or several kinds of littoral deposits (LEINZ and LEONARDOS, 1971; CHRISTOFOLETTI, 1974; FIGEIREDO, 1984; SUGUIO and TESSLER, 1984). Restinga as a Biome, including the integral part of major climate, vegetation belts and the animal species, was recognized by MÜLLER (1981, 1986). Such holistic view recognizes the Restinga as a complex system with several characteristic communities adapted to a range of prevailing environmental factors on Quaternary coastal zones.

The geological evolution of the Restinga in southernmost regions of Brazil has recently been studied by several authors (DELANEY, 1966; VILLWOCK, 1984; VILLWOCK et al., 1986; SUGUIO et al., 1986) that described a sequence of events related to the Quaternary climates. The flora is well characterized (MALME, 1936; RAMBO, 1954; REITZ, 1961; ESKUCHE, 1973; LINDEMAN et al., 1975; PFADENHAUER and RAMOS, 1979; PFADENHAUER, 1980; PORTO and DILLENBURG, 1986; WAECHTER, 1980, 1985, 1986; DILLENBURG, 1986) allowing the recognition of several zones and the possible origin of its elements. The faunal studies are scarce if not entirely absent for several groups. Only recently, studies have been conducted on rodents of the Restinga (XIMENEZ, 1980; TRAVI, 1981, 1983; FREITAS and LESSA, 1984; FREITAS et al., 1983, 1984; SBALQUEIRO et al., 1984; HAMEL, 1985; ZANCHIN, 1988; SBALQUEIRO, 1989; OLIVEIRA, 1985, 1991). With few exceptions (TRAVI, 1983; OLIVEIRA, 1985, 1991), a great amount of works are related to taxonomy and little information on habits and habitats of species are available.

The european colonization in Rio Grande do Sul began in the 18th century through the "caminho da praia"; a way along the Restinga in the coastal strip (THOMAS, 1976). In this region the first cattle farms were established near the coast. Certainly the quality of habitats have been

affected mainly by livestock grazing, and the extinction of almost all the large species of mammals by hunting was only one of the several consequences of the colonization. As a result, the zoogeographical features of the Restinga could be meaningfully interpreted only by the small fauna that survived in the highly patchy habitats. In contrast to the other families of small rodents present in the coastal areas in southern Brazil (Ctenomyidae, Caviidae, Echimyidae), apart from the commensals and the normally habitat-limited murids *Rattus* and *Mus* species, the small cricetids which have the advantage and ability to survive in small patches in almost all the landscape matrix, are useful for understanding the history of the Restinga. In such group, several species persist simultaneously in various habitat types allowing the analysis of some forces determining the species composition in the natural communities.

The present study is an attempt to analyse quantitatively the cricetid rodent faunal composition of several Restinga formations and neighbouring areas, and the effect of habitat structure and gradients on the assemblage's peculiarities. An effort has been made to assess the relative effect of habitat structure and species interaction on microhabitats partition and choices.

II. STUDY AREAS.

The Restinga's studied areas are located in southern Brazil, over the Geological Coastal Province of the Rio Grande do Sul (VILLWOCK, 1984), and in the extreme south of the Santa Catarina Island in the state of Santa Catarina. The Coastal Plain of Rio Grande do Sul, southwestern Santa Catarina, and northeastern Uruguay comprizes a strip of low lands with approximately 825 km long and maximum 120 km broad. The continual strip, almost without interruption is characterized by numerous lakes, lagoons, coastwise terraces, and dunes (DELANEY, 1960, 1966; SCHWARZBOLD and SCHÄFER, 1984; SUGUIO et al., 1986; SHÄFER, 1988). The west limits of such region in the south is demarkated by the Rio Grande do Sul - Uruguay Shield; a higher land system composed of Precambrian crystalline rocks (DELANEY, 1966). In the northeast of Rio Grande do Sul and southeast of Santa Catarina State the limits are the sedimentary and volcanic Mesozoic sequences which are part of the Paraná Basin and the Precambrian crystalline rocks of the Serra do Mar scarpment (VILLWOCK, 1984; VILLWOCK et al., 1986; SUGUIO et al., 1986). To the south of Santa Catarina Islands the narrow Restinga belt is limited by Precambrian crystalline hills of the Serra do Mar system (SUGUIO et al., 1986). In such region, the higher altitudes are the coastal active dunes that can reach up to 20 meters height (WAECHTER, 1985) and fixed dunes that can exceed 100 meters of elevation (VILLWOCK et al., 1986).

The sedimentation processes and morphology of the region were controlled by the Quaternary eustatic variation of sea level in the Upper Pleistocene and Holocene resulting in a complex system of sandy terraces (BIGARELLA, 1971; VILLWOCK, 1984; VILLWOCK et al., 1986; MARTIN et al., 1986; SUGUIO et al., 1986).

The west side of the Restinga is related to three major vegetation zones (Fig. 1): the (1) tropical and (2) subtropical forest, on western and southern slopes of the south-brazilian highlands respectively, and the (3) Pampean formations in the central and southern regions (HUECK and SEIBERT, 1981). In the latter, the open landscapes are dominated by undulating low hills. The forests normally form corridors along streams and rivers sometimes covering extensive areas. Isolated patches of subtropical forests in the Sul-riograndense Shield are close to the Restinga in the central region of the Coastal Plain. The Araucaria Forest and the grasslands of the South Brazilian Highlands are close to the Restinga, but isolated by the Atlantic Rain Forest and the scarpments of the Serra Geral and Serra do Mar.

In the Restinga, on the west side of the coastal strip, normally the landscape is formed by a mosaic of patchs of forests, swamps, and wet and dry grasslands contrasting with the sandy and treeless habitat types that compose almost a continuum from Uruguay to Santa Catarina. The vegetation, however, is believed to be originated from surrounding areas (RAMBO, 1954), at different times (SMITH, 1962), and no endemic species are commonly referred. In the northern region, before anthropogenic influences, the Atlantic Forest was the most extensive vegetational formation (RAMBO, 1951; VELOSO and KLEIN, 1963; WAECHTER, 1985). In the central and southern regions open vegetation as grasslands and swamps predominate in

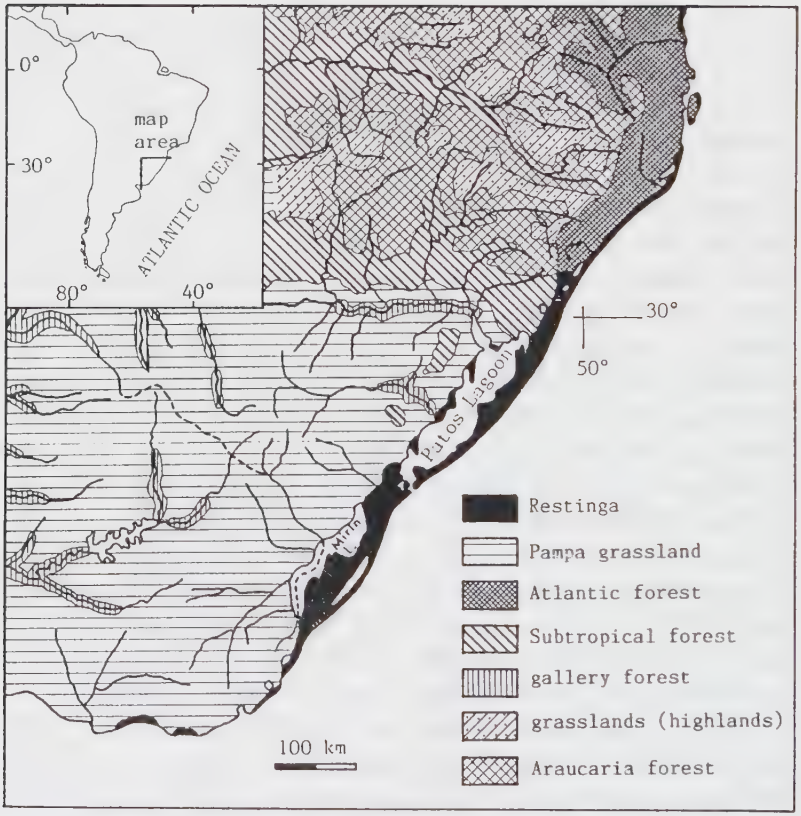
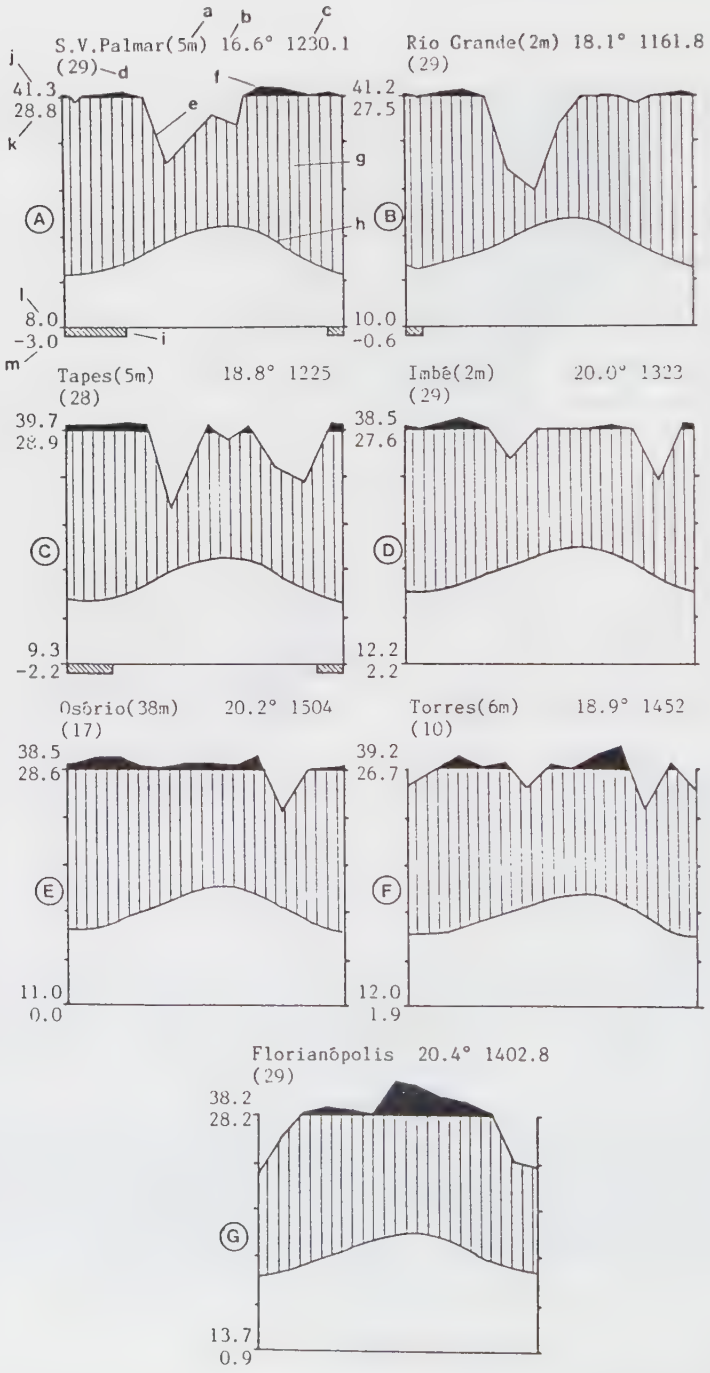


Fig. 1. Geographical location of Restinga and the major adjacent vegetation zones in the extreme South of Brazil and Uruguay (After HUECK and SEIBERT, 1981, modified).

the landscape (LINDMAN, 1906; RAMBO, 1954; PFADENHAUER and RAMOS, 1979; PFADENHAUER, 1980; MOHRDIECK, 1980; WAECHTER, 1985). Nevertheless, the complex vegetation zones of the Restinga can not be taken as seral successional stages due to its relative stability (PFADENHAUER, 1980).

The climate is humid and mild (Cfa - Köppen system) (MORENO, 1961; EIDT, 1968) (Fig. 2). From spring to summer, the southern position (28°S) of the Santa Helena anticyclone (subtropical semipermanent South Atlantic anticyclone) influences the plain and convective rainfall predominates. From autumn to winter, the Santa Helena anticyclone is shifted northward (to Tropic of Capricorn) and the polar cyclone, followed by polar migratory anticyclones, promotes frontal rainfall and lower temperatures (HASENACK et al., 1987).

Fig. 2. Climatograms for seven areas along the coast of Rio Grande do Sul and Santa Catarina. A) Santa Vitória do Palmar, near the extreme south of the Coastal Plain of Rio Grande do Sul; B) Rio Grande, in the extreme south of the Patos Lagoon; C) Tapes, in the west margin of the Patos Lagoon; D) Imbé, coastal area near the delta of the Tramandaí river; E) Osório, near the extreme south of the Atlantic forest; F) Torres, in the extreme north of the Coastal Plain of Rio Grande do Sul; G) Florianópolis, in the Santa Catarina Island. Abreviations: a) height above sea-level; b) mean annual temperature; c) mean annual precipitation in mm; d) duration of observations in years; e) curve of mean monthly precipitation; f) mean monthly precipitation > 100 mm (perhumid season); g) relatively humid season; h) curve of mean monthly temperature; i) month with absolute minimum below 0°C; j) highest temperature recorded; k) mean daily maximum of the warmest month; l) mean daily minimum of the coldest month; m) lowest temperature recorded. C, after GUERRA, 1988; D and E, after HASENACK et al., 1987; F, after WAECHTER, 1980.


a
b
c
S.V.Palmar(5m) 16.6° 1230.1
(29)
d
f
e
g
h
j
41.3
28.8
k
A
l
8.0
-3.0
m
i
Rio Grande(2m) 18.1° 1161.8
(29)
41.2
27.5
B
10.0
-0.6
Tapes(5m) 18.8° 1225
(28)
39.7
28.9
C
9.3
-2.2
Imbé(2m) 20.0° 1323
(29)
38.5
27.6
D
12.2
2.2
Osório(38m) 20.2° 1504
(17)
38.5
28.6
E
11.0
0.0
Torres(6m) 18.9° 1452
(10)
39.2
26.7
F
12.0
1.9
Florianópolis 20.4° 1402.8
(29)
38.2
28.2
G
13.7
0.9

The air circulation over the Coastal Plain is dominated by winds from the edges of the semipermanent South Atlantic anticyclone (EIDT, 1968). Winds from the northeast and east are frequent all over the year, but occasionally W, S and SE winds occur when cold air masses from the South reach to this region (NIMER, 1979).

Palynological evidences suggest a sequence of humid- and dry-climate intervals in the Late Pleistocene glacial stage in the coast of south Brazil (LORSCHEITER and ROMERO, 1985). Open and semiarborized landscapes (SOLIANI, 1973; PAULA COUTO, 1975) in the Late Pleistocene, and abundance of swamps in the early Würm (LORSCHEITER and ROMERO, 1985), were characteristic to the region. Such new data support the hypothesis that grasslands and swamps are old formations in the Coastal Plain and contrast with other authors (BIGARELLA and ANDRADE, 1965; AB'SABER, 1977) that have suggested a generalized semi-arid climate during this period.

1. INVESTIGATED AREAS (RODENTS/ENVIRONMENTAL VARIABLES)

1.1. TAIM

The southernmost sample site, the Taim Ecological Station (32° 32' S and 52° 32' W), is related to the lagoonal system of the Taim Swamp (SCHWARZBOLD and SCHÄFER, 1985) and is situated between the Mirim lagoon and the ocean. The annual precipitation ranges from 1,161.8 to 1,230.1 mm (Rio Grande, 55 km North, Santa Vitória do Palmar 128 km South - the two nearest weather stations along the coast) (MINISTÉRIO DA AGRICULTURA, 1969). Only in the end of spring and in summer the rainfall is lowered to less than 100 mm, causing dry periods (Fig. 2). The mean annual temperature ranges from 16.6°C to 18.1°C. In winter the absolute minimum can reach to -3°C.

The vegetation in the region ranges from almost naked dunes (Fig. 3) to forest on sandy terraces and swamp forest on the lower terraces with peat soils (WAECHTER, 1985; PORTO and DILLENBURG, 1986). However, the grasslands and the grassy swamps are the dominant formations (IRGANG et al., 1984; WAECHTER, 1985). Near the coast *Panicum racemosum* (POACEAE), *Hydrocotyle bonariensis* (APIACEAE) *and Paspalum vaginatum* (POACEAE) are dominant in the dune formations (COSTA et al., 1984). Clumps of *A. trigynum* (CYPERACEAE) cover extensive areas between the lakes and the ocean.

Fig. 3. Taim region. Coastal dunes with low cover of *Androtrichum trigynum* (CYPERACEAE). The low and wet areas near the forest present patches of *Eryngium pandanifolium* (UMBELLIFERAE).

The hydrological regime of the region is more determined by the geomorphological characteristics of the region than by the climate features (GOMES et al.,1987) that play a secondary role on the delimitation of the vegetation zones. In the sampled area in the north of the Taim Ecological Reserve (Fig. 4a), within the four vegetation types and ecotones (Fig. 4b), two habitat groups can be recognized in relation to the lagoonal

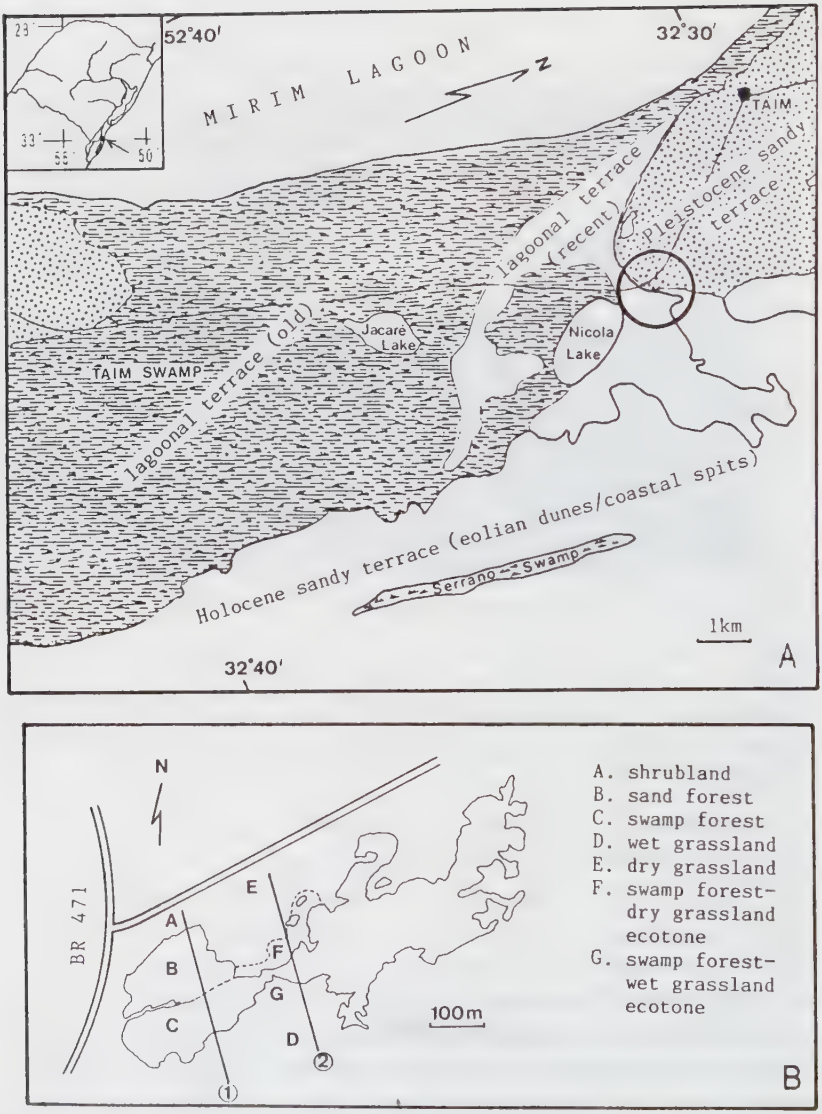


Fig. 4. Location map of the study area. A. Geological map with lagoonal and sandy terraces (After, GODOLPHIM, 1983, simplified) in the Taim region (the circle demarcates the sampled area); and B. the transect lines (1 and 2) in the extreme North of the Reserve.

system drainage and to the water table level: the habitats not subjected to periodic overflow - dry grassland and the sand forest - situated over a marine pleistocene terrace (GODOLPHIN, 1983); and those of swamp features - swamp forest and wet grassland - over a more recent lagoonal terrace with a level lower than the previous one. Both habitat groups are sharply separated by an inactive cliff (up to 1 m high) that delimites sandy and lagoonal terraces.

The dry grassland (Fig. 5) with sandy soils and high grass cover consists mainly of *Cynodon dactylon*, *Paspalum notatum*, *Bromus unioloides* and *Setaria geniculata*

Fig. 5. Dry grassland on sandy terrace and swamp forest on lower areas in the North of the Taim Ecological Reserve. Both habitats are sharply separated by and inactive cliff.

(POACEAE). The wet grassland is more heterogeneous than the previous ones. When overflowed, aquatic macrophytes such as *Eichhornia crassipes* (PONTEDERIACEAE) and *Pistia stratiotes* (ARACEAE) are abundant. *Eryngyum pandanifolium* (UMBELLIFERAE) is scattered or clumped among dense grass stands. Trees such as *Erythrina crista-galli* (LEGUMINOSAE) are scattered, with little effect on grass cover. The sand forest, adjacent to the dry grassland and a shruby area, presents sandy soil. The ground layer is dominated by *Oplismenus setarius*, *Pseudechinolaena polystachya*, *Panicum sp* (POACEAE) and scattered clumps of *Bromelia anthiacantha* (BROMELIACEAE). *Ficus organensis* (MORACEAE), *Sebastiana klotzschiana* (EUPHORBIACEAE) and *Randia armata* (RUBIACEAE) among others, are important trees on the forest structure (PORTO and DILLENBURG, 1986). The forest edge is composed mainly by *Opuntia vulgaris, Cereus peruvianus* (CACTACEAE), *B. anthiacantha* and *Myrrhinium lorantoides* (MIRTACEAE). The swamp forest in the lower terrace is composed mainly by *Erythrina crista-galli*, *F. organensis*, *Blepharocalix salicifolius* (MYRTACEAE) and *Sebastiana brasiliensis* (EUPHORBIACEAE). The undergrowth is composed mainly by graminoids, ferns, rushes and *Equisettum giganteum* (EQUISETACEA) (PORTO and DILLENBURG, 1986). Extensive muddy areas present no vegetation.

The livestock grazing suspended 5.5 years before the beginning of the work, led to an intensive enhancement of the ground layer density, particularly in the grassland habitat types.

1.2. CAPÃO DO LEÃO

The Capão do Leão region (31° 10' S, 50° 56' W) is located in the Mostardas Peninsula four kilometers northward from the Peixes Lagoon (Fig. 6), between the Patos Lagoon and the ocean. The study site is included in a region that presents the lowest annual precipitation of Rio Grande do Sul (IBGE, 1986) (less than 1,200 mm). The mean annual temperature ranges from 18°C to 19°C. The mean of the lowest temperatures of the coldest month (July) is below 9°C.

The region is composed by extensive Pleistocene sandy terraces and Holocene lagoonal terraces (CECO, 1988) parallel to the coast and oriented in a southwest-northeast direction. The lowlands (2-3 m above sea level) on lagoonal terraces, present wet grasslands composed mainly by graminoids and scatered clumps of *E. pandanifolium* and swamp forests (Fig. 7). Extensive areas are overflowed in wet periods but the forest sites present mesic conditions certainly due to artificial drain canals that attenuated its swampy features. The highlands (11-16 meters a.s.l.), composed by sandy terraces, present dry grasslands and sand forests. The dry grassland with low herb layer (usually less than 10 cm high) due to intensive livestock grazing, composes the largest portion of the region. The two forest types are contiguous and sharply separated by a high inactive cliff that delimits the sandy and the lagoonal terraces. *S. klotzschiana* and *Opuntia sp.* and *B. antiacantha* are important elements in the sand forest edge. The swamp forest ground layer is mainly composed by ferns and low forbs.

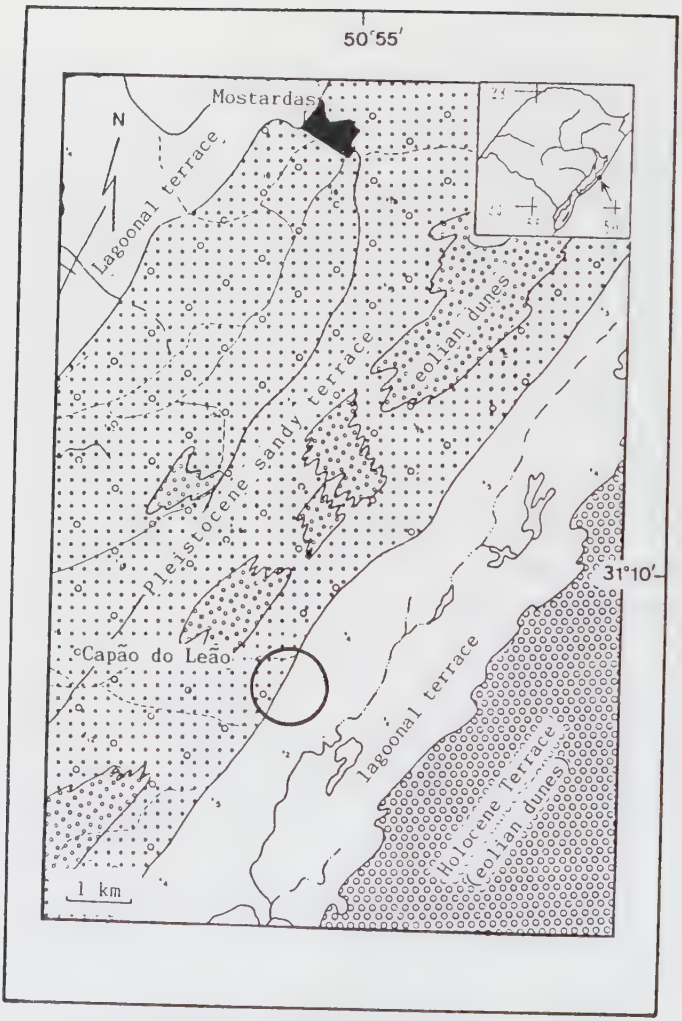


Fig. 6. Location map of the Capão do Leão region showing the sandy and the lagoonal terraces (After, CECO, 1988, modified). The circle demarcates the study area.

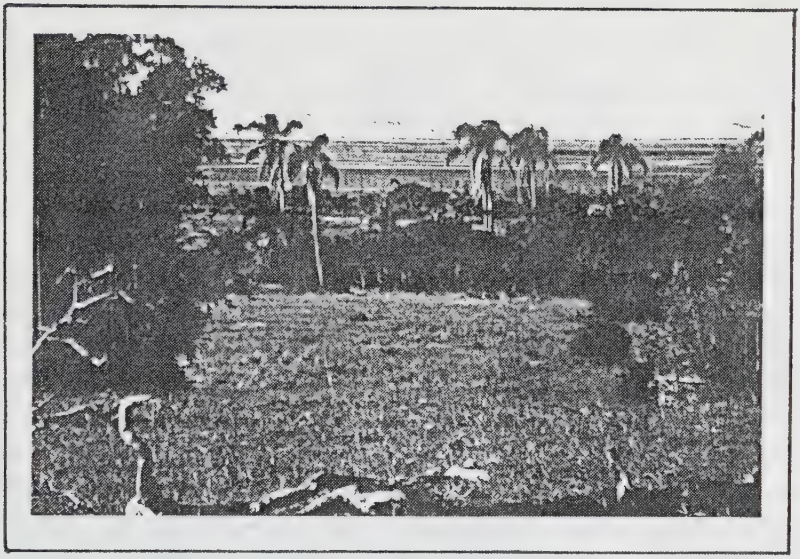


Fig. 7. Lowlands (on lagoonal terrace) in the Capão do Leão region showing grasslands and forests. The coastal dunes (background) are separated from the cited habitats by swamps and lakes. The palms are *Siagrus romansoffiana*.

1.3. FAXINAL

Faxinal region is situated in the extreme northeast of Rio Grande do Sul (29° 20' S, 49° 45' W) and 3 km southwestern from the town of Torres. A complex of Pleistocene and Holocene terraces (Fig. 8) (CECO, 1984) determines the drainage systems of the region and the vegetation zones. On lower sites, the tropical evergreen peat forest (WAECHTER, 1980) is the main formation (Fig. 9). Due to its flat and low topographic relief it is subjected to flooding over extensive areas. Notable trees are *F. organensis, Coussapoa microcarpa* (CECROPIACEAE), *Nectandra rigida, Ocotea pulchella* (LAURACEAE) and *Matayba guianensis* (SAPINDACEAE) among others (LINDEMAN et al., 1975; WAECHTER, 1980). The undergrowth is composed mainly by ferns, bromeliads and small forbs. On higher sandy terraces occur a Butiá savanna (*Butia capitata*) (ARECACEAE), the sand forest and the rain forest. The latters present a reduced area due to disruption by farming and logging. The region is near the southern limit of the Atlantic rain forest that extends along the coast of Brazil, and that migrated southward between the ocean and the south-brazilian highland slopes (RAMBO, 1950; VELOSO and KLEIN, 1968).

The mean annual precipitation is 1,452 mm, without dry periods (Fig. 2). The mean annual temperature is 18,9°C. The mean of the lowest temperatures of the coldest month (July) is 12°C (WAECHTER, 1980).

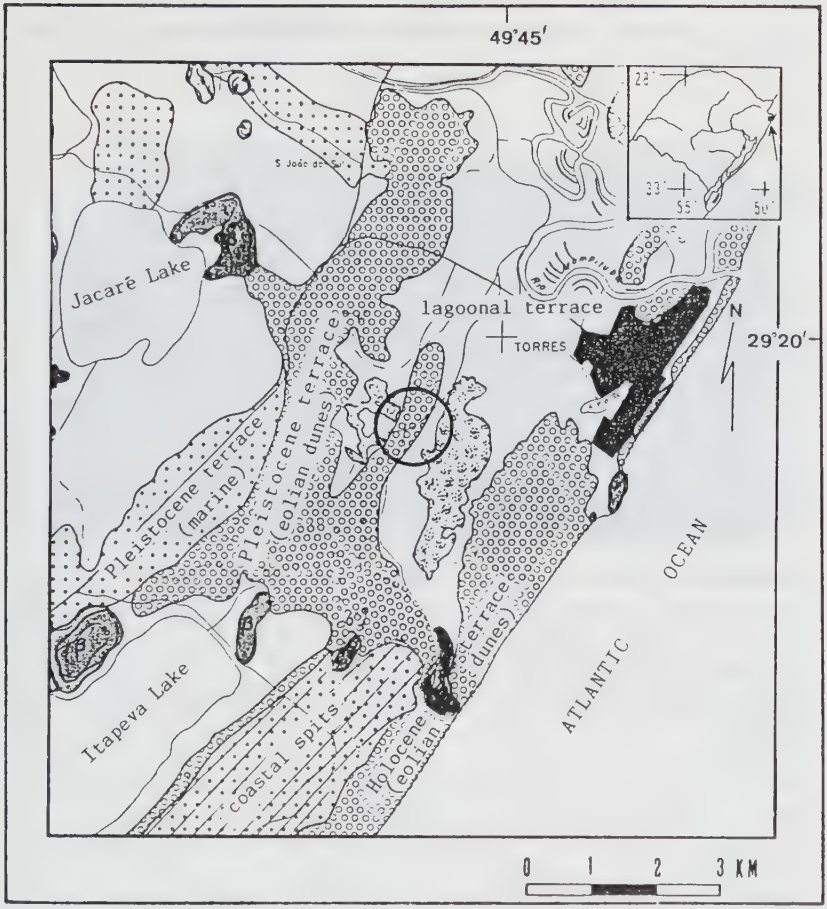


Fig. 8. Location map of the Faxinal region showing the sandy and the lagoonal terraces (After, CECO, 1984, modified) and the forest site studied (After, WAECHTER, 1980, modified). The circle demarcate the study area. β = Serra Geral formation.

Fig. 9. Swamp forest and shrubland in the Faxinal region, extreme North of the Coastal Plain of Rio Grande do Sul. Both habitat types are located on low terraces with peat soils.

1.4. COSTA DE DENTRO (SANTA CATARINA ISLAND)

The northernmost sampled site, Costa de Dentro (27° 46' S, 48° 31' W), in the south of the Santa Catarina Island (Fig. 10), in Santa Catarina State, is composed by a complex of vegetation types as swamp forests, rain forests, sand forests, woodlands and grassy swamps (Fig. 11). Areas of secondary growth are common in lower sites particularly in the rain forest on crystaline hill slopes. The lowlands on recent lagoonal and bay-bottom deposits, or marine sandy terraces (<5.100 years) (SUGUIO et al., 1986), are covered by grassy swamps, woodlands or sand forests and active and inactive dunes. Such areas are bordered by granite hills that in transgressive phases of eustatic variations of sea level composed an archipelago (MÜLLER, 1970). The tropical rain forest is the dominant vegetation formation on the hills. In such formation in the coast of Santa Catarina State, normally *Ocothea catharinensis* (LAURACEAE), *Sloanea guianensis* (ELAEOCARPACEAE), *Alchornea triplinervia* (EUPHORBIACEAE) and *Euterpe edulis* (ARECACEAE) are the dominant trees (KLEIN, 1978). In the swamp forest the undergrowth is composed mainly by *Calathea sp.* (MARANTACEAE), ferns and low graminoids. *Philodendrum sp.* (ARACEAE) and *Heliconia sp.* (ELICONIACEAE) are common urderstory elements.

The mean annual precipitation is 1,402.8 mm (Florianópolis town - 20 km north) without dry periods (Fig. 2). The mean annual temperature is 20.4°C. and the mean of the lowest temperatures of the coldest month (July) is 13.7°C (MINISTÉRIO DA AGRICULTURA, 1969).

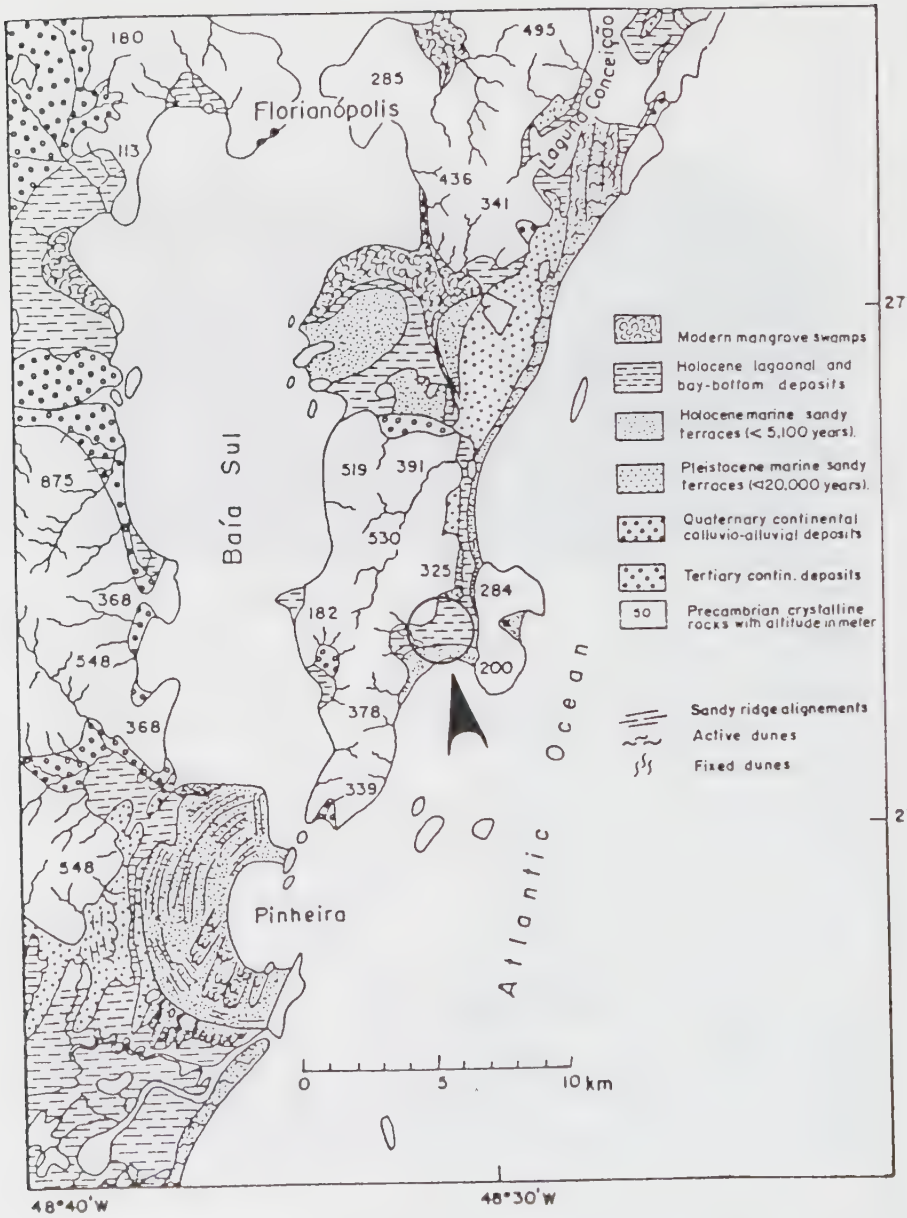


Fig. 10. Geological map of Ilha de Santa Catarina (After, SUGUÍO et al., 1986, modified). The arrow shows the study area.

Fig. 11. Swamp forest, grassy swamps on low areas and the rain forest on granite hills in the South of the Santa Catarina Island. The sand forest (background - right) is located near the ocean. The palms are *Syagrus romansoffiana*.

2. FURTHER SAMPLED AREAS (RODENTS SAMPLING ONLY)

Further sets of rodent sampling sites were selected along the Coastal Plain of Rio Grande do Sul and on the slopes of the south-brazilian highlands. In the Tramandaí Lagoon (29° 58' S, 50° 09' W), near the delta of Tramandaí river, Saco Mole, Lenha Seca and Imbé, sets of habitats composed by dunes, grasslands and salt marshes were sampled. The dune vegetation is composed mainly by *Androtrichum trigynum* (CYPERACEAE), *P. racemosum*, *Andropogon selloanus* (POACEAE) and *Hydrocotyle bonariensis* (APIACEAE) (PFADENHAUER and RAMOS, 1979; SOARES, 1984). The swamp areas are composed mainly by rushes and graminoids. Extensive areas are overflowed in wet periods, or by tidal waters and wind-induced waves.

In the west margin of Tramandaí Lagoon (Lenha Seca) and in the east margin of the Emboaba Lake (29° 58' S, 50° 13'W) two dense swamp forests were sampled. In such areas, in the mesic sites, the undergrowth is composed maily by ferns. In wetest sites *Calathea sp.* is the dominant element.

In the north of the Pinguela Lake and Palmital Lake (15 km northeast Osório town) two areas were sampled: Morro Alto (29° 46' S, 50° 11' W - 150 meters a.s.l.) and Pontal Palmital (29° 48' S, 50° 09' W). Morro Alto is related to the Serra Geral and covered by the Atlantic Forest in the slopes. Pontal Palmital is a sandy peninsula between Malvas Lake and Palmital Lake. The peninsula is partially covered by the lowland Atlantic Forest.

In Osório (29° 55' S, 50° 19' W), the extreme south of the Atlantic Forest, two areas were sampled: Morro Osório in the Serra Geral and a site on the Coastal Plain approximately 2 km southward of the Osório town. Such areas, separated by few kilometers, contrast by the abrupt changes in the topographic features and by vegetation cover. The first one is covered by the Atlantic Forest on hill slopes and the second by grasslands and patches of sand forest on the sandy plain.

On the southern slopes of the south-brazilian highlands (Sapiranga) two sites were sampled: Picada Verão (29° 35' S, 51° 02' W) and Alto Ferrabraz (29° 35' S, 50° 56' W - 550 meters a.s.l). Both are composed mainly by the rain forest and secondary growth formations resulting by logging. In sites of secondary growth, extensive areas are covered by low shrubs (*Baccharis sp.* - COMPOSITAE), graminoids and ferns (*Pteridium aquilinum* - POLYPODIACEAE). Shrubs, herbs, bamboos and giant ferns (*Dicksonia spp.* - CYATHEACEAE) compose, in some sites, a dense forest understory.

In the Pontal de Tapes, a sandy Holocene peninsula (JOST et al., 1974) (21 km long, 0.4-4.5 km width) in the west margin of the Patos Lagoon (30° 37' S, 51° 20' W) extensive sampling, among several habitat types, were performed. This strip lowland is covered by sand forests, swamp forest, grasslands and grassy swamps. In the northwestern portion the sand forests are mixed to a Butiá savanna. In the southern portion extensive areas are overflowed in wet periods but the habitats on higher terraces are less affected. The extensive grassy swamps are composed mainly by dense stands of rushes. At the lagoon margin *Scirpus californicus* (CYPERACEAE) and *Zizaniopsis bonariensis* (POACEAE) compose dense stands.

In the extreme southwest of the Patos Lagoon, in the Coastal Plain, an area near Pelotas town (31° 47' S, 50°

21' W) was sampled. Such area is composed by extensive swamps on alluvial sediments that are related to the drain basin of the Mirim Lagoon (JOST et al., 1974). The swamps (Banhado de São Gonçalo, Banhado do Alemão) are formed mainly by rushes (*Scirpus sp.*) and giant grass (*Z. bonariensis*). On sandy terraces, sand forests and grasslands are the principal formations. *Opuntia sp.* and *B. antiacantha* are important elements on the sand forest edges.

III. METHODS

1. SPECIES SAMPLING

In several study regions along the Restinga and adjacent areas in the slopes of the south-brazilian highlands, rodents were sampled by trap lines consisting of two wire mesh cages (9 by 9 by 22 cm) *per* trap site. Some variation in the lenght of the traplines existed (80 to 340 m) due to differences between the regions but the trap sites were always positioned 10m appart. Unsystematic, habitats outside the studied area were sampled to complement the information, by random allocation of traps or by selection of particular microhabitats. Traps were baited with fresh corn slices and a paste of peanut butter, industrialized fish meal, and oatmeal. In the two transect lines intercepting several vegetation zones and an inactive cliff in the Taim region (Fig. 4b) a standard mark-recapture data was colected. For each capture, species, sex and other pertinent data were noted. Each individual was numbered by toe clipping and ear cutting (FULLAGAR and JEWELL, 1965), and released at the point of capture. In the remaining regions the species were collected for taxonomic studies. All localities were sampled between July 1985 and August 1986, excepting Costa de Dentro and Capão do Leão that were sampled in autumn 1988.

2. HABITAT STRUCTURE MEASUREMENTS AND INDICES

In four regions (Taim, Capão do Leão, Faxinal and Costa de Dentro - Santa Catarina Island) microhabitats were characterized by measuring an array of 20 structural parameters (Tab. 1) at each trap site where an animal was captured. The sampling units centered on the traps consisted of two perpendicular 20-m^2 arm-length transects (Fig. 12), a 1.75-m^2 ring and four quarters around the trap site. All structural measurements were taken during the trap period exceptin one region (Taim) where they were measured only in the winter survey. The circle provided the measurements of foliage height density profile (FHD_{ij}) from ground level (2.5 cm) up to 170-cm height, for herbaceous and woody vegetation. The foliage height density calculated was based on the equation of ROSENZWEIG and WINAKUR (1969) with the following changes

$$FHD_{ij} = \sum \left[\frac{BCi + BCj}{2} \right] \left[h_i - h_j \right]$$

where BC_i is the mean cover (n=3) of a board of 5x10 cm at various heights above the ground (2.5, 12.5, 25, 50, 75, 100, 125, 150, 170 cm height) and at a horizontal distance of an arm-lenght (75 cm) from the trap site center. The cover scale was estimated according to DAUBENMIRE (1968) and the class proportion of cover midpoints (0.025, 0.15,

HHT	Herbaceous height.
HCV	Herbaceous cover.
FHD25	Foliage height density from 2.5 up to 25 cm.
FHD50	Foliage height density from 2.5 up to 50 cm.
FHD100	Foliage height density from 2.5 up to 100 cm.
FHD170	Foliage height density from 2.5 up to 170 cm.
CANHT	Canopy height.
CANCV	Canopy cover.
TDIA	Mean tree trunk diameter.
TDIS	Tree dispersion.
BRANCH	Mean tree branch height.
FLOG	Fallen logs importance.
SHRUB	Shrub density.
ROHIHO	Relative importance of potential rodents hiding holes (tree roots).
LIT	Relative importance of litter.
MUD	Relative importance of mud.
FLOOD	Relative importance of floods.
ROCK	% rock cover.
ROCAV	Relative importance of rock cavities.
SLOPE	Terrain slope angle.

Table. 1. Designation and description of habitat variables which were measured at each trap station where a capture occurred. For further information see text.

0.375, 0.625, 0.85, 0.975) means (Fig. 13) was used in the equation. The h_i and h_j are the heights. The index FHD_{ij} estimates the relative amount of foliage between heights i

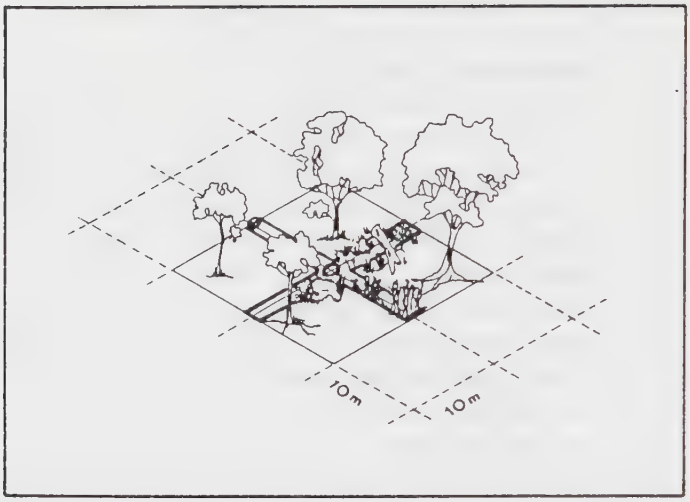


Fig. 12. Sample plot configuration.

and j. Observations for each quarter around the trap sites (COTTAN and CURTIS, 1956) provided the tree diameter (TDIA) (diameter at breast height $\geq$ 10 cm), first tree branch height (BRANCH), canopy height (CANHT), and tree dispersion (TDIS) (distance from traps of the nearest four trees). Since some trap sites were in forest edges or sites out the forests (with less than four trees in the quarters) the dispersion index was calculated as TDIS = NT / d, where NT is the number of trees (1, 2, 3 or 4) and d the mean distance or the distance to the nearest isolated tree. Such index (Fig. 14) allows the separation of forest trap sites with relative aggregation of trees from those at forest edges or in adjacent grasslands. The index may be interpreted as the relative importance of trees around the trap sites.

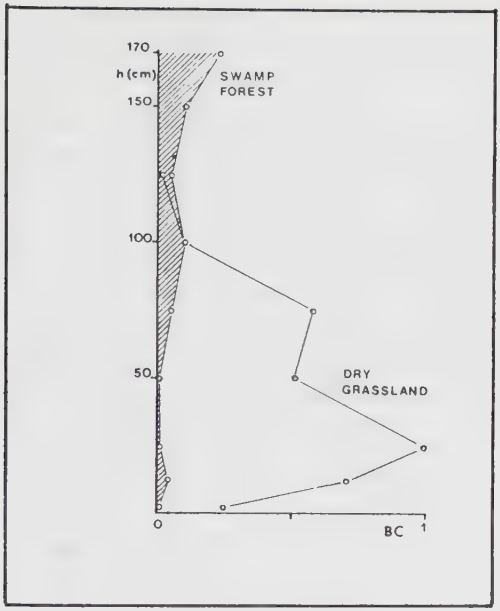


Fig. 13. Foliage height density (FHD_{ij}) profile in two sites (swamp forest and dry grassland). BC = mean board cover.

The two perpendicular transects provided the remaining measures. At each 2 meters along the transects the canopy cover (CANCV), herbaceous cover (HCV) and litter-soil cover were estimated by an ocular tube with cross wires. The cover was estimated according to DAUBENMIRE (1968) scale and the midpoint means (n = 21 *per* trap site) were used. The relative importance of litter (LIT) was estimated multiplying the proportion of cover by depth. The depth was measured directly from a graduated wire pushed through the litter. The relative importance of mud

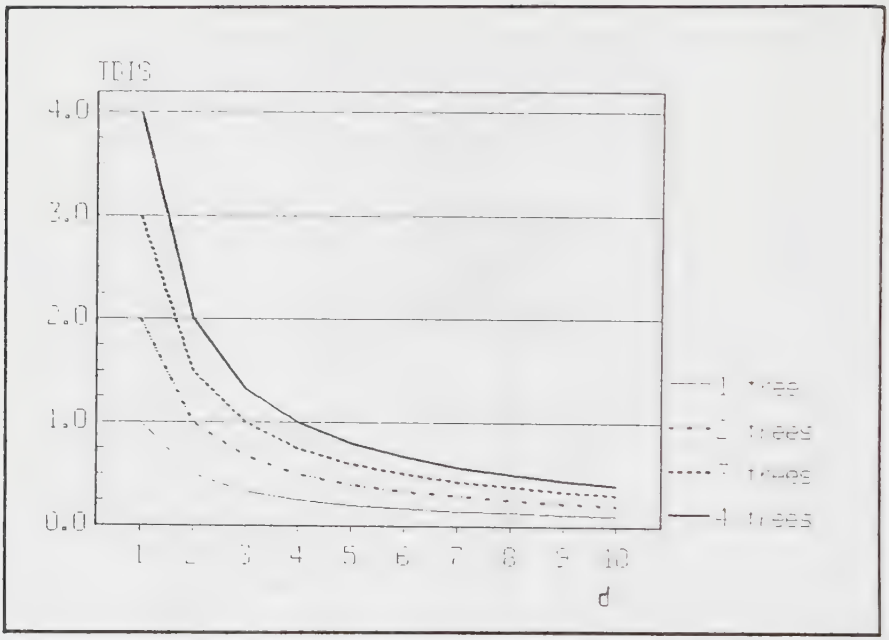


Fig. 14. Relationships between the tree dispersion index (TDIS) and the number of trees in the quarter around the traps.

(MUD), floods (FLOOD) and percentage of rock cover (ROCK) was estimated by showing downward and recording 21 plus or minus reading for the presence or absence of the variable (JAMES and SHUGART, 1970) along the transects. The variables relative importance of potential rodents hiding holes (in tree roots) (ROHIHO) and relative frequency of rock cavities (ROCK) estimate the availabilities of

shelters in which small mammals could be concealed. The variables were estimated by a subjective scale of importance (1, 2 or 3). The importance value was assigned at each observation along the perpendicular transects. The sum of scores represents the values of the variables in the sampled square. The fallen logs importance (FLOG) was calculated by the sume of fallen logs diameters ($\geq$ 10 cm) recorded along the transects. The shrub density (SHRUB) was the count of woody stems, with less than 10 cm diameter, that were intercepted by the outstretched arms along the two perpendicular arm-lenght transects (JAMES and SHUGART, 1970). The terrain slope was the measure of the highest declivity assigned by a clinometer centered on trap site.

3. QUANTITATIVE ANALYSIS

In this analysis, some methods were applied to stratified samples (habitat types) delineated by the physionomic characteristics of each unity (GAUCH, 1985). The vegetation zones were used as the main criterion for habitat recognition. In a second approach systematic samples (microhabitat types) were analysed without assigning trap sites to habitat categories and the species disclosed their habitat structural requirements with less influence of human preconception. Thus, trap sites were the unit analysed. However, a hybrid approach, stratified/

systematic, was used when all trap sites in selected habitats were included in the analysis.

In each region, all trap stations on the census lines were assigned to a habitat class. For each habitat category a capture index (CI_{tot} = NC / TD) was calculated pooling the number of captures (NC) and considering the number of trap days (TD). The trap days included two revision by day (early morning and late afternoon) to avoid bias by potential diurnal species. The CI_{tot} for Taim differed from the other regions by including captures and recaptures.

The niche breadth (NB) was calculated according to LOMOLINO (1984) using the proportion of trap stations falling into the habitat categories. The NB ranges from zero, where the species is restricted to a single habitat type, to a maximum value of 1, where the species proportionally uses all the habitat categories.

A replicated and non replicated goodnes-of-fit test (G) (SOKAL and ROHLF, 1981; ROHLF, 1988) was used for examination of microhabitat selection among the rodent species. The proportion of trap days from all habitat types was used to calculate the expected proportion of captures among the habitats. The null hypothesis is random capture frequencies across available habitats.

All the similarities (faunal similarity among the areas based on rodents taxonomic composition; habitat structural distances based on means of environmental variables; habitat or species distances based on ordination scores) were calculated by the Euclidean distance

$$d_{jk} = \sqrt{\sum (d-j)^2}$$

where d and j are the species occurrence (1) or absence (0), mean values of environmental variables, or the scores obtained by the ordination analysis in paired samples. The resulting matrix were summarized in dendrograms performed by the UPGMA (unweighted pair-group method using arithmetic averages) clustering method, using the CLUSTER ANALYSIS routine of SPSS (SPSS/PC+, 1988). The dendrograms were then compared to the original matrix to compute the coefficients of cophenetic correlation (r_{cd}), which reflect the accuracy of the distance values in the dendrograms in relation to those in the distance matrix (SNEATH and SOKAL, 1973). The major similarity groups in each analysis were delimited by a "phenon line" that represents the mean of the Euclidean distances scores in the original matrix.

The relations between the various environmental variables with the number of species caught (NSC) by habitat type, and the species capture index (CI_{tot}) were investigated by the Pearson's product moment correlation coefficient (r) and by multiple regression analysis (stepwise procedure) (SPSS/PC+, 1988).

The species-environment relationships analysis were performed by the Canonical Correspondence Analysis (CCA) (TER BRAAK, 1986, 1987a, JONGMAN et al., 1987). Such direct gradient analysis in which species occurrences are related directly to environmental variables (GAUCH, 1985), select the linear combination of environmental variables that maximize the dispersion of the species scores (TER BRAAK, 1987b). The data on species composition are explained through a Gaussian response model (GAUCH and WHITAKER, 1972; TER BRAAK and PRENTICE, 1988) in which the explanatory variable is a linear combination of the environmental variables. The species scores resulting from the analysis actually estimate the optima (centroids) of the species in the model. Thus the species abundance or

probability of occurrence decreases with distance from its location in the diagram. The species distribution with respect to an environmental variable is the average of the values of that environmental variable at those sites at which the species occurs (TER BRAAK and LOOMAN, 1986). The scores obtained from CCA for each analysis were displayed in biplots where arrows represent the environmental variables and the points the species scores. The cosine between arrows and species (points) angle provides an approximation of the Pearson's correlation coefficient. Consequently, arrows that point in the same direction indicate positive correlation, perpendicular arrows indicate lack of correlation and arrows pointing in the opposite direction indicate negative correlation between species and environmental variables. The order of the perpendicular projection of species points on variable axis approximates to the ranking of the weighted averages of the species with respect to the environmental variables (TER BRAAK, 1986). The differences in weighted averages between species indicate differences in their distribution along that environmental variable.

The classification of trap sites based on sample scores that are derived from the species scores and from the linear combination of environmental variables allows the analysis of the species environment relationships. The correlation between the species axis and the environmental axis in the CCA is the species-environment correlations (Ter BRAAK, 1986). The mean of trap site scores which are linear combinations of environmental variables, and formerly assigned to habitat class, was used to calculate the habitat centroids.

A student t-test (MONTGOMERY and PECK, 1982; TER BRAAK, 1987a) was used to select subsets of environmental variables that explain the species distribution almost equally well as the full set. When the t-values were not

significant the regression coefficient of the variable not differed from 0 and the variable does not contribute significantly to the regression.

The assessment of habitat components effect on rodent distribution was carried out by partial Canonical Correspondence Analysis fitting variable sets as covariables. The significance of the ordinations was tested by the Monte Carlo permutation test (MCpt) by randomly permuting the sample numbers in the environmental data, and giving rise to a "random data set" (HOPE, 1968; TER BRAAK, 1987a).

All the environmental variables were standardized to unit variance after log-transformation.

The multiple regression procedure to estimate the unique effects of the set of habitat and species variables, respectively, was based on DUESER and PORTER (1986) by using the direct regression approach of HALLET and PIMM (1979)

$$N_{1h} = z - \beta_{12}{}^{*}N_{2h} - \beta_{13}{}^{*}N_{3h} - \ldots - \beta_{1n}{}^{*}N_{nh}$$

$$+ \beta_{11}H_{1h} + \beta_{12}H_{2h} + \ldots + \beta_{1n}H_{nh}$$

where N_{nh} is the density of each species in h trap site, z is the intercept and the β^{*} are the partial regression coefficients corresponding to the effect of each species on the first after the effects of habitat have been taken into account. The β's are the partial regression coefficients corresponding to each habitat variable.

One multiple regression analysis was conducted for each species, using the REGRESSION routine of SPSS (SPSS/PC+, 1988). The number of captures of each species at a station was used in each separate regression model. The dependent

variable was the frequency of capture of the species at the trap stations where a capture of any species was recorded. In each model the independent variables included the number of captures and the environmental variables. The hypothesis that the real change in R^2 is 0 can also be formulated in terms of β parameters (SPSS/PC+, 1988) therefore, significant change in R^2 can be interpreted as significant species interactions. The analysis estimates the unique effect of the sets of habitat and species variables respectively.

The overall squared multiple semipartial correlation coefficients (R_{hs}^2) express the total explained variation in the dependent species when all habitat and species variables are included in the analysis. The habitat coefficients (R_h^2) are the change in the overall coefficients that occurs when the habitat variables are added to a model that already contains the species variables. The species interaction coefficients (R_s^2) are the changes in the multiple semipartial coefficients for the species variables, after entering the environmental variables in the first step. The ratio

$$\frac{R_h^2 - R_s^2}{R_{hs}^2}$$

is the proportion of the observed variation in the species captures accounted for the habitat (R_h^2) and the species variables (R_s^2) (COHEN and COHEN, 1975; DUESER and PORTER, 1986). The more positive the total variance (%) attributable to habitat and species variables the larger the abundances influenced by the habitat variables.

The regression analysis was used to generate a community matrix (HALLETT and PIMM, 1979; HALLET, 1982) that estimates the interaction coefficients between species pairs.

IV. RESULTS AND DISCUSSION

1. THE RODENT ASSEMBLAGES' SIMILARITIES

1.1. SPECIES ACCOUNT

Twenty species of cricetid rodents were captured along the Coastal Plain of Rio Grande do Sul, Santa Catarina Island, and in the south-brazilian highland slopes in Rio Grande do Sul (Tab. 2). This section gives a brief account of each species based on literature records, and samples not analysed by the microhabitat approach. The mean weight of each species and the macroniches (EISENBERG, 1981) based on the feeding adaptation and substrate categories is assigned to each species based on my own observations and by consulting different sources (DAVIS, 1947; MOOJEN, 1952; CABRERA and YEPES, 1960; MASSOIA, 1964; BARLOW, 1969; REIG, 1980; PIZZIMENTI and DE SALLE, 1980; MYERS and CARLETON, 1981; ALHO, 1982; CRESPO, 1982; NOWAK and PARADISO, 1983; ANDERSON and JONES, 1984; MESERVE et al., 1988).

The macroniche is based on modal tendencies at the generic level, rather than the full spectrum the species can show throughout annual cycle (EISENBERG, 1981). However, when data are available the macroniches may refer to species. When cited only for the first species it is related to the genus, except when mentioned. Some species are assigned to more than one substrate category because some of them may occur in dry sites as coastal dunes or swampy grasslands with extensive and permanent overflowed

	OXYRUF	OXYIHE	OXYHIS	OXYROB	DELKEM	AKONIG	AKOCUR	AKOAZA	AKOSER	BOLLAS	SCATUM	ORYFLA	ORYDEL	ORYNIG	ORYNIT	ORYRAT	NECSQU	HOLBRA	CALLAU	DELDOR
1.Costa de Dentro			*				*					*		*	*	*	*			
2.Faxinal		*				*	*			*				*		*				
3.Alto Ferrabraz		*				*	*					*		*			*			*
4.Picada Verão		*		*		*	*			*		*		*	*		*			*
5.Morro Alto							*							*		*				
6.Pontal Palmital							*					*		*		*				
7.Morro Osório		*					*			*				*	*	*				
8.Osório										*				*						
9.Emboaba					*									*		*				
10.Imbé					*							*						*		
11.Lenha Seca					*									*		*		*		
12.Saco Mole					*							*						*		
13.Delta Tramandaí					*							*						*		
14.Pontal de Tapes	*				*		*						*					*		
15.Capão do Leão											*	*	*			*		*		
16.Banhado do Alemão								*	*		*	*	*					*		
17.Taim	*				*			*	*		*	*	*					*	*	

Table 2. Rodent species and sampled areas along the Coastal Plain of Rio Grande do Sul, Santa Catarina Island and in the slopes of south-brazilian highlands. OXYRUF = *Oxymycterus rufus*, OXYIHE = *O. iheringi*, OXYHIS = *O. hispidus*, OXYROB = *O. roberti*, DELKEM = *Deltamys kempi*, AKONIG = *Akodon nigrita*, AKOCUR = *A. cursor*, AKOAZA = *A. azarae*, AKOSER = *A. serrensis*, BOLLAS = *Bolomys lasiurus*, SCATUM = *Scapteromys tumidus*, ORYFLA = *Oryzomys flavescens*, ORYDEL = *O. delticola*, ORYNIG = *O. nigripes*, ORYNIT = *O. nitidus*, ORYRAT = *O. ratticeps*, NECSQU = *Nectomys squamipes*, HOLBRA = *Holochilus brasiliensis*, CALLAU = *Calomys laucha*, DELDOR = *Delomys dorsalis*.

areas. Thus the macroniches as employed here not imply necessarily in an adaptation (e.g semiaquatic or scansorial features) but, therefore, in habitat used. The assignment approximates the species peculiarities in the study region.

Voucher specimens collected have been deposited at the Departament of Genetics, University of Rio Grande do Sul, Porto Alegre. Additional informations about the populations and individuals studied in this work are available in reports cited in this section and marked by an asterisk (*).

Oxymycterus rufus (Fischer, 1814) - 54.4 g (n=20). Macroniche: terrestrial/ insectivore-omnivore. The species occurs in Paraguay, northeast and eastern Argentina, Uruguay, and southern Brazil (LANGGUTH, 1966; VITTULO et al., 1986; HAMEL, 1985*; OLIVEIRA, 1985*)

Oxymycterus iheringi Thomas, 1896 - 35.5 g (n=10). Occurs in the Atlantic Forest from eastern and southern Brazil to subtropical forest of northeast Argentina (HENSEL, 1872; THOMAS, 1896, 1902; MASSOIA, 1963).

Oxymycterus hispidus Pictet, 1843 - 99.8 g (n=6). The species occurs in east and southern Brazil and northeast Argentina (CABRERA, 1961; HONACKI et al., 1982). According to CABRERA (1961) and REIG (1987) *O. hispidus* includes other species described for southern Brazil (*O. judex* Thomas, 1909 and *O. questor* Thomas, 1903) and northeast Argentina (*O. missionalis* Sanborn, 1931).

Oxymycterus roberti Thomas, 1901 - 70 g (n=1). The species is found in east, central (THOMAS, 1901; VIEIRA, 1955; REDFORD, 1984; MARES et al., 1986) and southern Brazil (this work). In Central Plateu region in the

Cerrado dominion, the species is found in moist grasslands near gallery forests and springs (ALHO, 1982). In southern Brazil the species was found in areas of secondary growth.

Deltamys kempi Thomas, 1917 - 19.1 g (n=20). Macroniche: terrestrial-semiaquatic/ insectivore-omnivore. Occurs in Uruguay and islands of the Parana Delta between Uruguay and Argentina (THOMAS, 1917a; MASSOIA, 1964; XIMENEZ et al., 1972) and southern Brazil (SBALQUEIRO et al., 1984*). The genus *Deltamys* has been included as a subgenus of *Akodon* (MASSOIA, 1964; REIG, 1987), but in this work the genus is used according to THOMAS (1917), MASSOIA (1981), HAMEL (1985*), SBALQUEIRO et al. (1984*), and SBALQUEIRO (1989*).

Akodon nigrita (Lichtenstein, 1829) - 23.5 g (n=4). Macroniche: terrestrial/insectivore-omnivore. The species occurs in south and eastern Brazil and northeast Argentina (MASSOIA, 1962,1963, VIEIRA, 1955) and Paraguay (MYERS and WETZEL, 1979).

Akodon cursor (Winge, 1887) - 28.3 g (n=20). The species occurs in Uruguay, northeastern Argentina, southern Paraguay and eastern and southern Brazil (XIMÉNEZ and LANGGUTH, 1970; REIG, 1987; LIASCOVICH and REIG, 1989). The complex taxonomy and systematics of *A. cursor* were discussed and revised by REIG (1987).

Akodon azarae (Fischer, 1829) - 21.1 (n=20). Occurs in Uruguay (XIMÉNEZ et al., 1972) and also in central and northeast Argentina, Bolivia, and Paraguay (REIG, 1964; FORNES and MASSOIA, 1965; CRESPO et al., 1970; CONTRERAS, 1973; MYERS and WETZEL, 1979; HONACKI et al., 1982). The species is normally associated to open landscapes (DALBY, 1975; O'CONNELL, 1982) but may occur in sand forest in the

Restinga of southern Brazil (OLIVEIRA, 1985*). Cytogenetic and enzymatic studies have been conducted recently in a population of the Coastal Plain (HAMEL, 1985*; SBALQUEIRO, 1989*). The species occurs also in southwest of Rio Grande do Sul (LANGGUTH, 1965).

Akodon serrensis Thomas, 1902 - 29.0 g (n=20). The species is found in the Atlantic Forest in the Serra do Mar in the Paraná State, and subtropical forests of northeastern Argentina (THOMAS, 1902; JUSTO and SANTIS, 1977; ZOTZ, 1985; ZOTZ et al., 1985; LIASCOVICH and REIG, 1989; SBALQUEIRO, 1989*). Cytogenetic and enzymatic studies have been conducted recently comparing the populations of the Coastal Plain of Rio Grande do Sul and the Serra do Mar in the Paraná State (HAMEL, 1985*; SBALQUEIRO et al., 1985*; SBALQUEIRO, 1989*).

Bolomys lasiurus (Lund, 1841) - 26.6 g (n=4). Macroniche: terrestrial/herbivore-granivore. The species occurs in many habitats south of the Amazon (HERSHKOVITZ, 1962), central, northeast and eastern Brazil, Paraguay and Bolivia (MACEDO and MARES, 1987). The taxonomy and systematics of the genus *Bolomys* are discussed by REIG (1987) and APFELBAUM and REIG (1989). SBALQUEIRO (1989) provides information about two populations in south Brazil.

Scapteromys tumidus (Waterhouse, 1837) - 103.8 g (n=20). Macroniche: semiaquatic/ insectivore-omnivore. The species occurs in lowlands of southern Brazil (HENSEL, 1872; FREITAS et al., 1984*, OLIVEIRA, 1991*), Uruguay, northeastern Argentina and southern Paraguay (MASSOIA and FORNES, 1964; HERSHKOVITZ, 1966; MYERS and WETZEL, 1979). The relationships between populations of southern Brazil

(FREITAS et al., 1984*), Uruguay and Argentina (BRUM-ZORRILLA et al., 1986) have been recently analysed.

Oryzomys flavescens (Waterhouse, 1837) - 14.7 g (n=20). Macroniche: terrestrial/herbivore. The species occurs in Uruguay, south Brazil, and central and northeastern Argentina (CABRERA, 1961; HONACKI, 1982). SBALQUEIRO (1989*) provides cytotaxonomic data about populations of south Brazil.

Oryzomys delticola Thomas, 1917 - 25.6 g (n=20). Macroniche: scansorial/-. The species occurs in Uruguay, in savannas and subtropical forests of northeastern Argentina (CABRERA, 1961; MASSOIA and FORNES, 1967; XIMENEZ et al., 1972; MARCONI and KRAVETZ, 1986), and in Rio Grande do Sul (OLIVEIRA, 1985*, 1991*, HAMEL, 1985*; SBALQUEIRO, 1989*). *O. delticola* is closely related to *O. nigripes* regarding the number and morphology of the chromosomes (SBALQUEIRO, 1989*; ZANCHIN, 1988*). The taxonomic relations of both taxa need to be reviewed.

Oryzomys nigripes (Olfers, 1818) - 26.4 g (n=20). Macroniche: scansorial/-. The species occurs in Paraguay, northern Argentina (MYERS and CARLETON, 1981), and southeastern Brazil (ZANCHIN, 1988*). *O. nigripes* is closely related to *O. delticola* regarding the number and morphology of the chromosomes (ZANCHIN, 1988*; SBALQUEIRO, 1989*). The taxonomic relations of both taxa are not clear and the relationships of several populations in southern Brazil need a comprehensive review.

Oryzomys nitidus (Thomas, 1884) - 67.3 g (n=4). Macroniche: terrestrial/-. Occurs in the Andes of Ecuador, Peru, Bolivia, northwest Argentina and southern Brazil (GARDNER and PATTON, 1976; HONACKI et al., 1982; NOWAK and

PARADISO, 1983). The individuals captured in the south-brazilian highland slopes in Rio Grande do Sul have been compared with populations of eastern Brazil (ZANCHIN, 1988*).

Oryzomys ratticeps Hensel, 1873 - 104 g (n=11). Macroniche: terrestrial/-. Occurs in forests of Paraguay, northeastern Argentina, and southern and eastern Brazil (IHERING, 1892; HENSEL, 1872; THOMAS, 1902; CABRERA, 1961; MASSOIA and FORNES, 1962; AVILA-PIRES and GOUVEA, 1977). Recent cytotaxonomic studies have compared populations from southern and eastern Brazil (ZANCHIN et al., 1987*, ZANCHIN, 1988*).

Nectomys squamipes (Brants, 1827) - 201 g (n=7). Macroniche: semiaquatic/omnivore. Occurs from northwestern South America (Guianas to Colombia and Peru) to Paraguay, northeastern Argentina (CABRERA, 1961; HONACKI et al., 1982), and from northeast to southern Brazil (MAIA et al., 1984*).

Holochilus brasiliensis (Desmarest, 1819) - 130.6 g (n=6). Macroniche: semiaquatic/herbivore. Occurs in Paraguay, northeastern Argentina, Uruguay, southern, central and eastern Brazil (HONACKI et al., 1982; NOWAK and PARADISO, 1983; FREITAS et al., 1983*).

Calomys laucha (Olfers, 1818) - 14.8 g (n=2). Macroniche: terrestrial/herbivore. Occurs in Uruguay (XIMENEZ et al., 1972), central Argentina, southern Bolivia, and Paraguay (HERSHKOVITZ, 1962; MASSOIA et al., 1968; OJEDA and MARES, 1989). In Rio Grande do Sul the species was found also in the south of the Patos Lagoon (IHERING, 1892) and in the southwest of the Rio Grande Shield (Bagé) in heavily overgrazed pastures.

Delomys dorsalis (Hensel, 1872)- 22.6 g (n=2). Macroniche: terrestrial/-. Occurs in south and eastern Brazil and northeastern Argentina (HENSEL, 1872; MASSOIA, 1962; VIEIRA, 1955; SBALQUEIRO, 1989*). The species is normally assigned to genus *Thomasomys* (HONACKI et al., 1982; NOWAK and PARADISO, 1983), but THOMAS (1917) and ÁVILA-PIRES (1960a, 1960b) considered *dorsalis* in genus *Delomys*. SBALQUEIRO (1989*) provides cytotaxonomic data about two populations in southern Brazil.

1.2. FAUNAL SIMILARITIES

The evaluation performed in seventeen areas along the Coastal Plain, and in the south-brazilian highland slopes in Rio Grande do Sul and in the Santa Catarina Island, demonstrated that the rodent fauna is differently composed particularly along the coast. The species composition varies markedly from North to South and West to East resulting from a complex interplay of historical and ecological factors. In the northern region, in the lowlands and on the Serra do Mar and Serra Geral eastern slopes, the Atlantic Forest is the principal vegetation formation (RAMBO, 1951; VELOSO and KLEIN, 1963; KLEIN, 1978; WAECHTER, 1985). In the central and southern regions open vegetation as grasslands and swamps predominate in the landscape (LINDMAN, 1906; RAMBO, 1954; PFADENHAUER and

RAMOS, 1979; PFADENHAUER, 1980; MOHRDIECK, 1980; WAECHTER, 1985). Such vegetation pattern allows the expectancy that the rodent fauna may be closely related to the dominant vegetation zones.

Three major groups of areas, based on the rodent assemblages taxonomic distance, are clearly recognized ($d_{jk}<\overline{d_{jk}}$) (APPENDIX 1) showing the composite nature of the region (Fig. 15). A high cophenetic correlation coefficient was observed (r_{cd}=0.790, n=136, P<0.001). The southernmost similarity group resembles more to the Pampean Province (FITTKAU. 1969; CABRERA and WILLINK, 1980) and the Uruguayan centre of MÜLLER (1973) which extends its range from southern Brazil and Uruguay to eastern Argentina. Such group of areas contain some rodent species like *O. rufus, A. azarae, C. laucha, S. tumidus,* and *D. kempi* normally related to open landscapes, and assemblages with high similarity with the Uruguayan fauna and eastern Argentina (compare XIMENEZ et al., 1972; CABRERA, 1961; MASSOIA, 1961, 1964; MASSOIA and FORNES, 1967; MARCONI and KRAVETZ, 1986). Northern elements as *A. serrensis* and *O. ratticeps*, common to the Atlantic Forest in the Serra do Mar and subtropical forest of northeastern Argentina, occur in southern forest sites that compose isolated patches on extensive grassland, sandy, or swamp areas. This could be taken as an evidence that the forests along the coast might act as corridors for some tropical elements. The population of *A. serrensis* in the extreme south of the Coastal Plain is notable. The species was not found in northern Restinga regions, where apparently it is replaced by *A. cursor*. However, *A. serrensis* may occur in the Rio Grande Shield by looking at the records in southwest of the Patos Lagoon. The causes of non-overlaping distribution need further investigations since both species appear to be allopatric and pottentialy occupy similar habitats. Both species were not found in a

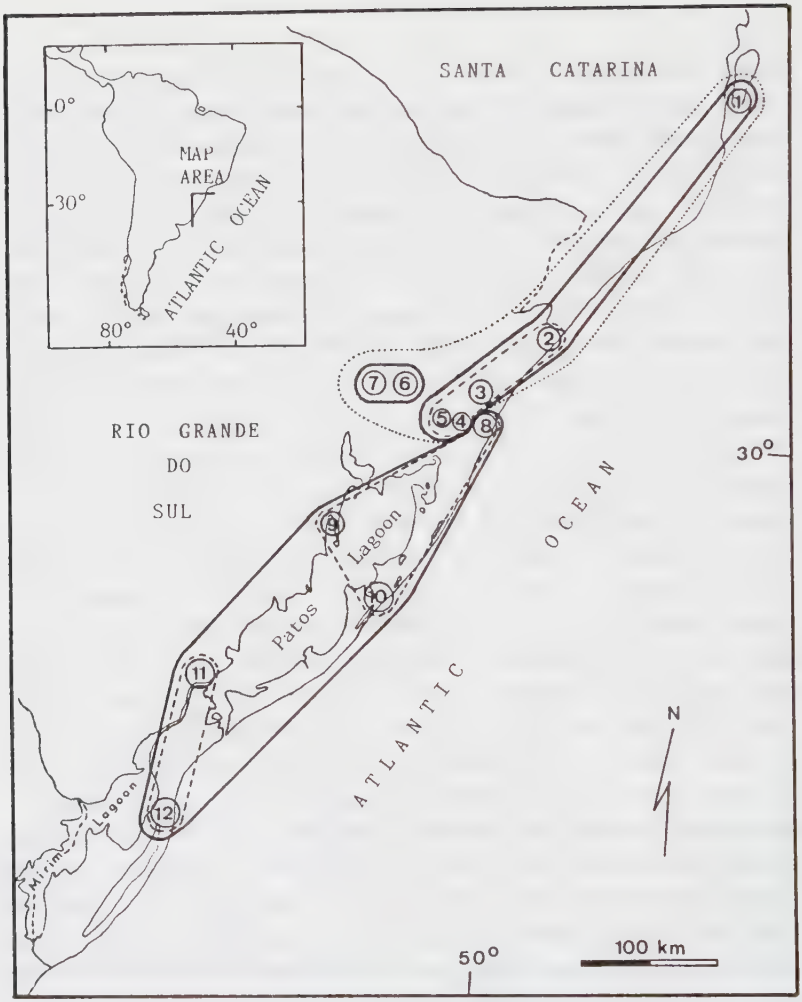


Fig. 15. Regional affinities based upon rodent taxonomic composition. The continuous lines delimit the groups with mean Euclidean distance below the mean of the original distance matrix ($\bar{d}_{jk}$). The dashed lines delimit the subgroups with d_{jk} below (---) and above (...) the mean. 1. Costa de Dentro (Santa Catarina Island); 2. Faxinal; 3. Morro Alto and Pontal Palmital; 4. Emboaba and Lenha Seca; 5. Morro Osório and Osório; 6. Alto Ferrabraz; 7. Picada Verão; 8. Imbé, Saco Mole, Delta of the Tramandaí river; 9. Pontal de Tapes; 10. Capão do Leão; 11. Banhado do Alemão; 12. Taim. r_{cd} = 0.790 (cophenetic correlation).

large central zone in the Coastal Plain of Rio Grande do Sul.

The southern Restinga rodent fauna may be more complex due to the occurrence of some species not recorded in the present work (and not included in the analysis), but present near the western margin of the Patos Lagoon as *Thomasomys oenax* Thomas, 1928 and *Wiedomys pyrrhorhinus* (Wied-Neuwied, 1821) (IHERING, 1892; THOMAS, 1928; PINE, 1980). However, no information is available about the distribution of these species in such regions where the subtropical forests of the Coastal Plain and the Rio Grande Shield are close to each other.

The other two major groups of similarity are composed by several areas situated in the northern region of the Coastal Plain, in the slopes of the south-brazilian highlands, and in the Santa Catarina Island. Both groups are close and more related within themselves than to the group of southern regions. The rodent assemblages in northern Restinga and in the Santa Catarina Island are more tropical, and consist of several species that extend their distribution to northern regions of South America. The forest elements are common, some of them occurring in open formations composed largely by a complex of seral stages resulting from human disturbance. Nevertheless, the assemblages of the north portion of the coast showed high similarity to those found in the south-brazilian highland slopes. This fact is in close agreement with the flora pattern that is composed mainly by tropical elements derived from neighbouring areas (RAMBO, 1954; SMITH, 1962; WAECHTER, 1985). In the Santa Catarina Island the rodent fauna presents similar pattern. However, the treeless habitats as extensive grassy swamps and sandy grasslands are poor in species. Important to note is that in this region grassland-rodents were not found. Such observation contrasts greatly with southern regions where the

assemblages are composed partially by elements related to forests and by others more related to grassland habitat types. The southern elements are largely absent in the north of the Coastal Plain of Rio Grande do Sul and in the Santa Catarina Island, with exception of *O. flavescens*. However, this species may be taken as a habitat generalist and is normally found in a variety of habitats in southern Brazil. On the other hand, the taxonomical status of the small *Oryzomys* species (subgenus *Oligoryzomys*) is poorly understood and the relationships of several populations need to be reviewed.

The boundaries of the biogeographic provinces are acentuated in the north of the Coastal Plain of Rio Grande do Sul between Osório and Torres. In such transitional regions the variation showed by rodent assemblages composition is partially related to the abrupt changes in the topographic features due to the presence of the Serra Geral. A west-east gradient is largely molded by the importance of the lowland forests and by the decrease in frequency of open landscapes. Recent disruption of lowland forests leads to extensive secondary grassland or shrubland formations. However, in such areas the rodent assemblages approximated the composition of northern regions. Near the coast, in the delta of Tramandaí river, in extensive swamps and grasslands, the rodent fauna is related to southern regions.

In a north-south gradient the Restinga represents a interface between tropical and subtropical regions since the composite rodent fauna reflects major continental patterns. However, the west-east gradient is closely related to local ecological conditions, partially determined by the geological history of the Coastal Plain.

2. THE RODENTS AND THE HABITAT RELATIONS

2.1. TAIM

2.1.1. OVERALL HABITAT STRUCTURAL SIMILARITIES

The overall structural similarity between the habitats considering the mean values of the variables (Tab. 3) showed two general groups: forest and grassland (Fig. 16). The forest habitat types are more dissimilar than the grassland types, but compose an unit. The grassland group comprises of two subgroups, each one with elements of high structural similarity ($d_{jk} < \overline{d_{jk}}$-s). Although the grassland features predominate, the two forest-grassland ecotones show high structural similarities and are separated from the forest groups.

2.1.2. HABITAT GRADIENTS

The canonical coefficients and the correlations of the environmental variables with the axis (Tab. 4) in the canonical ordination (CCA) showed that the first axis is a forest-dry grassland gradient. The forest sites show low

Habitat Variable	SPF	SDF	STW	STD	SBL	WEG	DRG
HHT	27.08	11.16	66.38	71.52	17.33	36.36	43.24
HCV	35.50	55.32	85.42	84.22	65.48	93.25	92.71
FHD25	5.72	5.15	18.80	16.19	13.23	19.36	19.52
FHD50	10.31	8.49	34.50	29.89	18.01	30.81	36.97
FHD100	15.33	15.26	47.80	45.71	21.51	35.87	49.43
FHD170	20.19	22.21	62.94	49.95	25.73	36.38	50.08
CANHT	7.04	7.45	4.08	3.95	0.00	0.00	0.00
CANCV	55.50	66.64	1.64	8.33	0.00	1.67	0.00
TDIA	40.60	40.41	34.24	29.69	0.00	0.00	0.00
TDIS	0.92	0.84	0.25	0.48	0.14	0.19	0.05
BRANCH	1.46	2.12	0.95	0.71	0.00	0.00	0.00
FLOG	10.83	1.38	3.60	2.40	0.00	0.00	0.00
SHRUB	9.81	2.12	3.00	8.00	1.83	3.06	0.00
ROHIHO	5.71	0.43	0.00	0.40	0.00	0.11	0.00
LIT	1.08	1.80	3.42	1.28	2.02	2.04	1.05
MUD	14.19	0.00	4.40	10.00	0.00	2.23	0.00
FLOOD	46.10	0.00	33.40	23.80	0.00	56.06	0.02

Table 3. Sample estimates of the mean for the seventeen habitat variables for each habitat type. The variable acronyms are from Tab. 1. SPF = swamp forest; SDF= sand forest; STW= swamp forest - wet grassland ecotone; STD= swamp forest - dry grassland ecotone; SBL= shrubland; WEG= wet grassland; DRG= dry grassland.

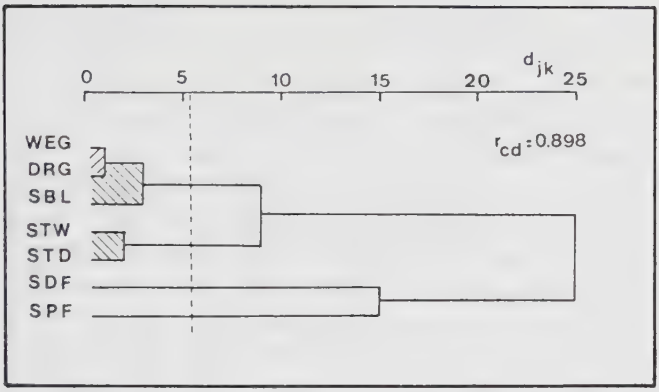


Fig. 16. Dendrogram of habitat structural relationships. d_{jk} = structural distance (Euclidean distance - rescaled). The dashed line represents the mean Euclidean distance ($\overline{d_{jk}}$). The diagonal shading areas demarcate the groups with high structural similarity ($\overline{d_{jk}}$-s). WEG = wet grassland; DRG = dry grassland; SBL = shrubland; STW= swamp forest - wet grassland ecotone; STD= swamp forest - dry grassland ecotone; SDF= sand forest; SPF = swamp forest. r_{cd} = cophenetic correlation.

ground cover and wet or dry soil, whereas the grassland sites, in the other extreme of the gradient, show high ground cover, high foliage height density (up to 25 and 50 cm high) and dry soil. The second axis is a gradient ranging from the forest with dry sites and low herb layer to grass areas with high herbaceous height, high foliage density (up to 170 cm high), and high ground cover. The HHT variable is associated more with wet and low canopy cover sites at the swamp forest edges. This variable is

	Canonical coefficients				Correlation coefficients			
AXIS	1	2	3	4	1	2	3	4
variable								
HHT	-0.01	0.04	-0.01	-0.02	0.05	0.65	0.03	-0.07
HCV*	0.08	0.00	0.01	-0.01	-0.28	0.37	0.18	0.02
FHD25*	-0.10	0.00	0.06	0.11	-0.37	0.53	0.07	-0.03
FHD50*	0.13	0.04	-0.07	-0.24	-0.30	0.55	0.08	-0.12
FHD100	-0.11	-0.02	0.08	0.19	-0.19	0.54	0.11	-0.10
FHD170	0.05	0.00	-0.03	-0.07	-0.05	0.52	0.13	-0.08
CANHT	-0.06	-0.06	0.04	0.01	0.48	-0.28	0.10	-0.04
CANCV	0.04	0.00	0.05	-0.01	0.39	-0.47	0.07	-0.07
TDIA*	0.07	0.02	-0.05	0.01	0.47	-0.15	0.01	0.04
TDIS*	0.05	0.03	-0.05	0.02	0.48	-0.10	-0.13	-0.02
BRANCH*	0.01	0.00	0.06	-0.04	0.50	-0.24	0.18	-0.08
FLOG	-0.01	-0.01	0.01	-0.01	0.19	-0.19	0.04	-0.08
SHRUB*	0.05	0.01	0.00	0.01	0.38	0.04	-0.24	0.02
ROHIHO	0.03	0.00	-0.02	-0.02	0.27	-0.26	-0.12	-0.07
LIT*	0.03	0.01	0.03	0.04	0.09	0.21	0.36	0.18
MUD	0.02	-0.01	0.01	0.00	0.35	0.11	-0.17	-0.03
FLOOD*	0.00	0.04	0.03	0.01	0.24	0.37	0.17	0.02

Table 4. Canonical coeficients and intra-set correlations of environmental variables with the first four axis of canonical correspondence analysis (CCA) for Taim winter data. The environmental variables were standardized to unit variance after log-transformation. Variable acronyms are from Tab. 1. * = variables with t-value <0.05.

low correlated with the first axis, that explains the main gradient, and can be taken as the extreme of a secondary gradient. Together with foliage height density from 2.5 to 170 cm high (FHD170), the herbaceous height characterizes the wet ecotones between the swamp forest and the grassland.

The ordination depicted by the diagram (Fig. 17) has an environmental basis and shows the variation and complexity of the landscape. The mean scores of the CCA, which are linear combination of environmental variables (TER BRAAK, 1986) considering the trap sites in each recognized habitat, showed a major habitat gradient from the right to the left hand of the diagram. Although the degree of similarity (dissimilarity = Euclidean distance) between the habitats varies greatly, three groups are clearly evident (criterion $d_{jk}<\overline{d_{jk}}$) by the cluster analysis of the distance matrix of the CCA scores (tab. 5). A high cophenetic correlation was observed ($r_{cd}=0.834$, $P<0.001$).

	SPF	SDF	SBL	STW	STD	DRG	WEG
SPF	0.00						
SDF	1.60	0.00					
SBL	2.12	2.53	0.00				
STW	0.99	2.59	2.42	0.00			
STD	1.37	2.88	2.05	0.66	0.00		
DRG	2.25	3.17	0.97	2.12	1.55	0.00	
WEG	1.80	3.16	1.73	1.29	0.63	1.01	0.00

$\overline{d_{jk}}=1.85$

$s=0.78$

Table 5. Euclidean Distance (d_{jk}) between the habitat centroids related to first and second CCA axis. The habitat acronyms are from Tab. 3.

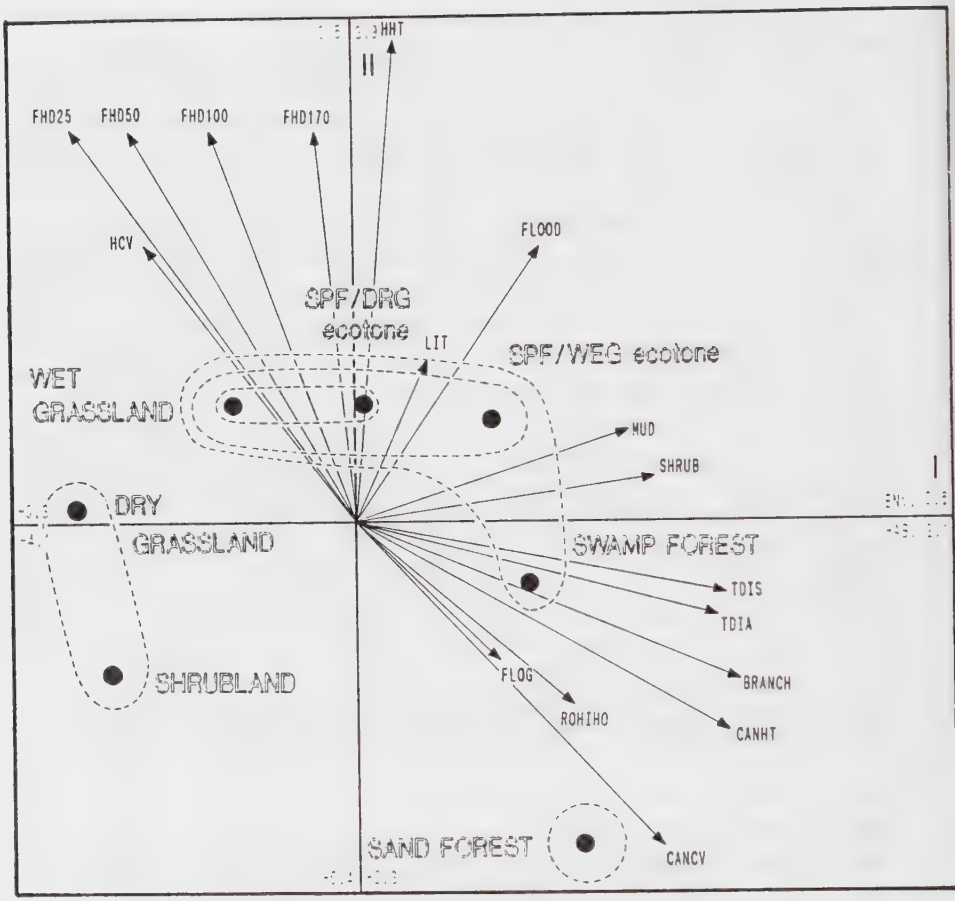


Fig. 17. Canonical Correspondence Analysis (CCA) diagram with habitat centroids on the first two axis for the Taim region (70 trap sites). The centroids are the mean scores of the CCA which are linear combination of environmental variables. The dotted lines delimit the three groups whose Euclidean distance between the centroids is less than the mean ($\overline{d_{jk}}$) of the distance matrix (cf. Tab. 5). For further information see Methods. The variable acronyms are from Tab. 1.

The three clusters with similarity greater than the mean similarity of the full set are disposed along the axis 1, and are refered here as the "forest-dry grassland gradient". They reflect the complexity nature of the region. The axis extremities are formed by the swamp forest, wet grassland and the ecotones, that compose a particular group. This intermediate cluster includes four related habitat types where three of them (swamp forest / wet grassland and swamp forest / dry grassland transitions, and wet grassland) are more related to the second axis. The centroids of the forests (sand forest and swamp forest) lie at the bottom-right-hand corner of the diagram. Both habitats share common variables that characterize woody sites but they are not in the same cluster, mainly due to the gradual transition from the swamp forest to the wet grassland. The degree of similarity varies with the axis employed and indicates different trends in other less clear gradients. Only the shrubland near the extreme of the main gradient appears to be a particular seral stage. Certainly this area will progress toward a sand forest, the ultimate stage under these condictions. The other habitat types can be considered as series of stages of the ecocline in a more stable or in the end point of succession.

2.1.3. RODENTS HABITAT USE

The total capture of rodents (CItot) in the surveyed habitats revealed some trends in summer and in winter

seasons (Fig. 18). In winter it tends to decrease inside the forest and increase in the transitional habitats and in the other grassland habitat types. In the summer the highest CI_{tot} was obtained in the swamp forest, contrasting with the winter when the highest index was observed in the swamp forest - grassland transitional microhabitats and in the shrubland. This suggests that in the winter the forest habitat types may be less suitable to the community as a whole than the grasslands. The increasing flood in the swamp forest and the low availability of shelters in the sand forest may be partially responsible for the observed pattern.

The niche breadth of the species, taking into account the sampling distribution of habitats, was generally stable between both the seasons. Only *O. delticola* increasingly used the available habitats from summer to winter, approximating to the niche breadth of *O. serrensis* and *S. tumidus* (Fig. 19), the two species with the broadest niche. Only *O. rufus* and *A. azarae* used to a lesser degree the available habitats.

The pooled analysis of the replicated goodness-of-fit test was significant in summer and winter (G_p=67.39, G_p=42.41, d.f.=6, $P<0.01$, respectively) and showed that the whole rodent community occupied the microhabitats in frequencies different from their availabilities (Tab. 6). In the summer the swamp forest was clearly suitable and the wet and dry grasslands appeared to be avoided (Fig. 20). In the winter only the sand forest and the wet grassland were negatively selected.

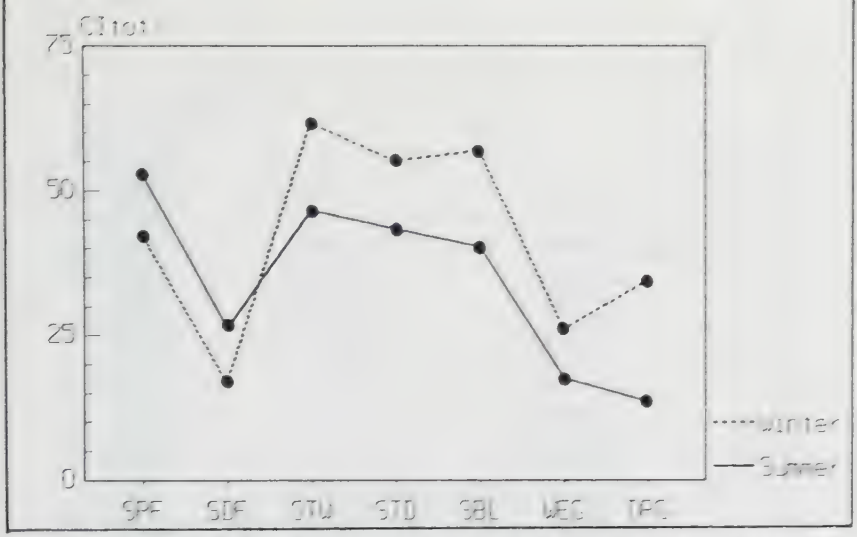


Fig. 18. Capture index (CI_{tot}) of total species expressed as function of seasons and habitats (absolute values in Table 6). SPF = swamp forest; SDF = sand forest; STW = swamp forest - wet grassland ecotone; STD = swamp forest - dry grassland ecotone; SBL = shrubland; WEG = wet grassland; DRG = dry grassland.

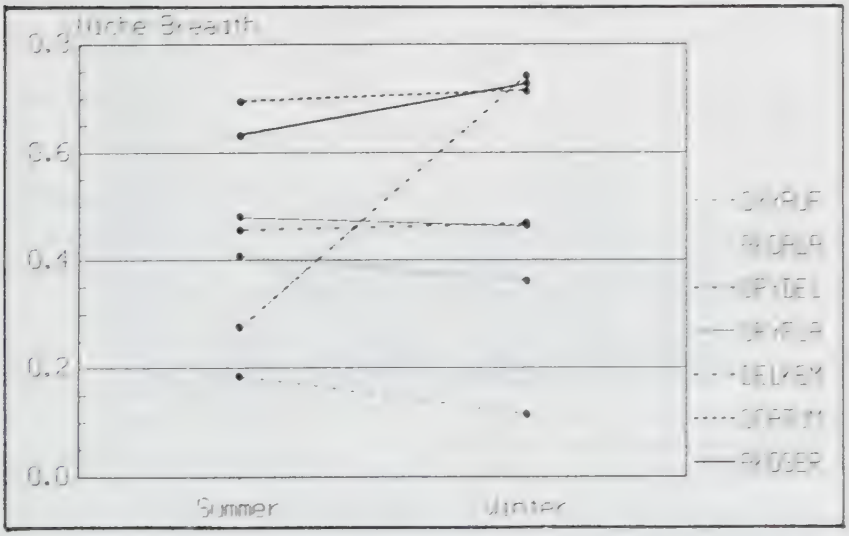


Fig. 19. Species niche breadth expressed as function of seasons. The niche breadth ranges from 0, where the species is restricted to a single habitat type, to a maximum of 1, where the species indiscriminantly uses all habitats. OXYRUF = *O. rufus*; DELKEM = *D. kempi*; AKOAZA = *A. azarae*; AKOSER = *A. serrensis*; SCATUM = *S. tumidus*; ORYFLA = *O. flavescens*; ORYDEL = *O. delticola*.

	SUMMER	WINTER	TOTALS
	Obs./Exp.	Obs./Exp.	Obs./Exp.
SPF	133/86.7	106/96.0	239/182.7
	(52.8)	(42.1)	
SDF	22/28.9	14/32.0	36/60.9
	(26.2)	(16.7)	
STW	28/20.6	37/22.9	65/43.5
	(46.7)	(61.7)	
STD	26/20.6	33/22.9	59/43.5
	(43.3)	(55.0)	
SBL	29/24.8	41/27.4	70/52.2
	(40.3)	(56.9)	
WEG	38/74.3	56/82.3	94/156.6
	(17.6)	(25.9)	
DRG	13/33.0	33/36.6	46/69.6
	(13.5)	(34.4)	
TOTALS	289	320	609

Table 6. Total number of observed (Obs.) and expected (Exp.) captures of rodent species by habitat categories in summer and winter surveys. In parentheses the total index of captures. The habitat acronyms are from Tab. 3.

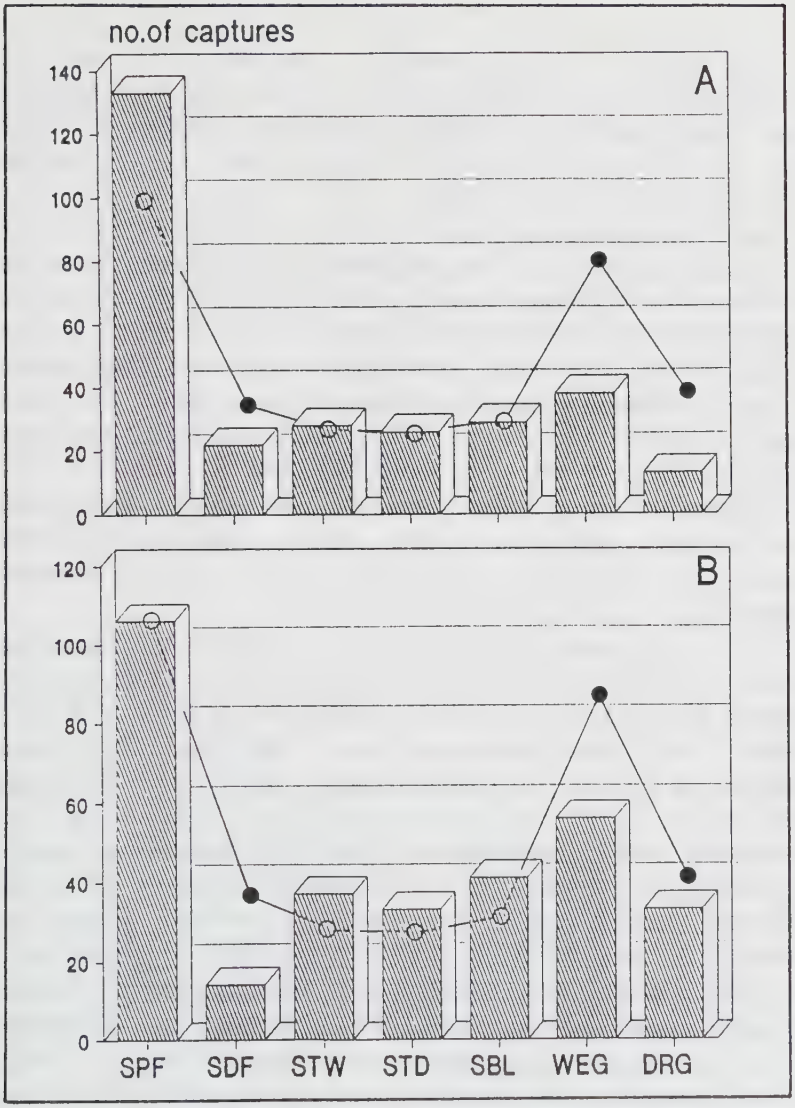


Fig. 20. Observed and expected number of total captures of rodents in seven habitats in the Taim region for summer (A) and the winter (B) (cf. Tab. 6). SPF = swamp forest; SDF = sand forest; STW = swamp forest - wet grassland ecotone; STD = swamp forest - dry grassland ecotone; SBL = shrubland; WEG = wet grassland; DRG = dry grassland.

The tables 7 and 8 summarize the number of captures observed for each habitat type in summer and in winter. The heterogeneity G, calculated on the tallied captures for all species by habitat category, was significant in the two seasons (G_H=210.86, G_H=183.77, d.f.=30, P<0.001; summer and winter respectively), indicating that the obtained captures in the microhabitats deviated from the expected in a heterogeneous manner. The total G for the summer (G_T=278.56, d.f.=30, P<0.001) partitioned in its additive component parts showed that no single species was a microhabitat generalist (P<0.01) at least in this period. The total G for the winter was significant (G_T=226.36, d.f.=36, P<0.001) but two of its additive components, *S. tumidus* and *O. delticola*, used the microhabitats in proportions which did not differ from their availability, and contrasting with the summer season.

The whole community did not use the three major habitat types - forest, ecotones, and grassland - in proportion of their availability (G_p=54.32, G_p=28.44, d.f.=2, P<0.001; summer and winter respectively). The heterogeneity G indicated that the species included in the analysis (five in summer, and six in winter) (Tab. 7 and Tab. 8) deviated from the expected capture frequencies in a heterogeneous manner (G_H=147.68, d.f=8; G_H=93.91, d.f.=10; P<0.001, respectively). Only in the winter one species, *S. tumidus*, appears as a habitat generalist (G_{adj}=0.75, d.f.=2, P>0.25) (Fig. 21 a and b). All the others showed some restriction in using the habitats and a strong positive selection to some of them (P<0.05).

S. tumidus is normally associated with wet areas (MASSOIA and FORNES, 1964; BARLOW, 1969; SIERRA DE SORIANO, 1969; MILLER and ANDERSON, 1977) but is able to explore several habitat types (XIMENEZ and LANGGUTH, 1971; OLIVEIRA, 1991). The captures were always more

	SPF	SDF	STW	STD	SBL	WEG	DRG	TOTALS
O. rufus				2			5	7
				(3.3)			(5.2)	
D. kempi	1		4	3		10		18
	(0.4)		(6.7)	(5.0)		(4.6)		
A. azarae			1		2	1		4
			(1.7)		(2.8)	(0.5)		
A. serrensis	121	22	10	15	25	5		198
	(48.0)	(26.2)	(16.7)	(25.0)	(34.7)	(2.3)		
S. tumidus	10		7	6		5	2	30
	(4.0)		(11.7)	(10.0)		(2.3)	(2.1)	
O. flavescens	1		4			17	4	26
	(0.4)		(6.7)			(7.9)	(4.2)	
O. delticola			2		2		1	5
			(3.3)		(2.8)		(1.0)	
H. brasiliensis							1	1
							(1.0)	
NSC	4	1	6	4	3	5	5	
Totals	133	22	28	26	29	38	13	289
Trapdays	252	84	60	60	72	216	96	840

Table 7. Taim region. Number of captures of each species by habitat categories in summer. Three species, *A. azarae*, *O. delticola*, and *H. brasiliensis*, were excluded from the replicated goodness-of-fit test because of small sample sizes. In parentheses, the capture index CI(%) based on trapdays *per* habitat. NSC = number of species caught. The habitat acronyms are from Tab. 2.

	SPF	SDF	STW	STD	SBL	WEG	DRG	TOTALS
O. rufus							5	5
							(5.2)	
D. kempi	1		12	6		10	1	30
	(0.4)		(20.0)	(10.0)		(4.6)	(1.0)	
A. azarae					16	5	10	31
					(22.2)	(2.3)	(10.4)	
A. serrensis	83	5	21	22	23	27	8	189
	(32.9)	(6.0)	(35.0)	(36.7)	(31.9)	(12.5)	(8.3)	
S. tumidus	7		2	4		3	3	19
	(2.8)		(3.3)	(6.7)		(1.4)	(3.1)	
O. flavescens	1					5	5	11
	(0.4)					(2.3)	(5.2)	
O. delticola	14	9	2	1	2	6	1	35
	(5.6)	(10.7)	(3.3)	(1.7)	(2.8)	(2.8)	(1.0)	
NSC	5	2	4	4	3	6	7	
Totals	106	14	37	33	41	56	33	320
Trapdays	252	84	60	60	72	216	96	840

Table 8. Taim region. Number of captures of each species by habitat categories in winter. *O. rufus* was excluded from the replicated goodness-of-fit test because of small sample size. In parentheses, the capture index CI (%) based on trapdays *per* habitat. NSC = number of species caught. The habitat acronyms are from Tab. 2.

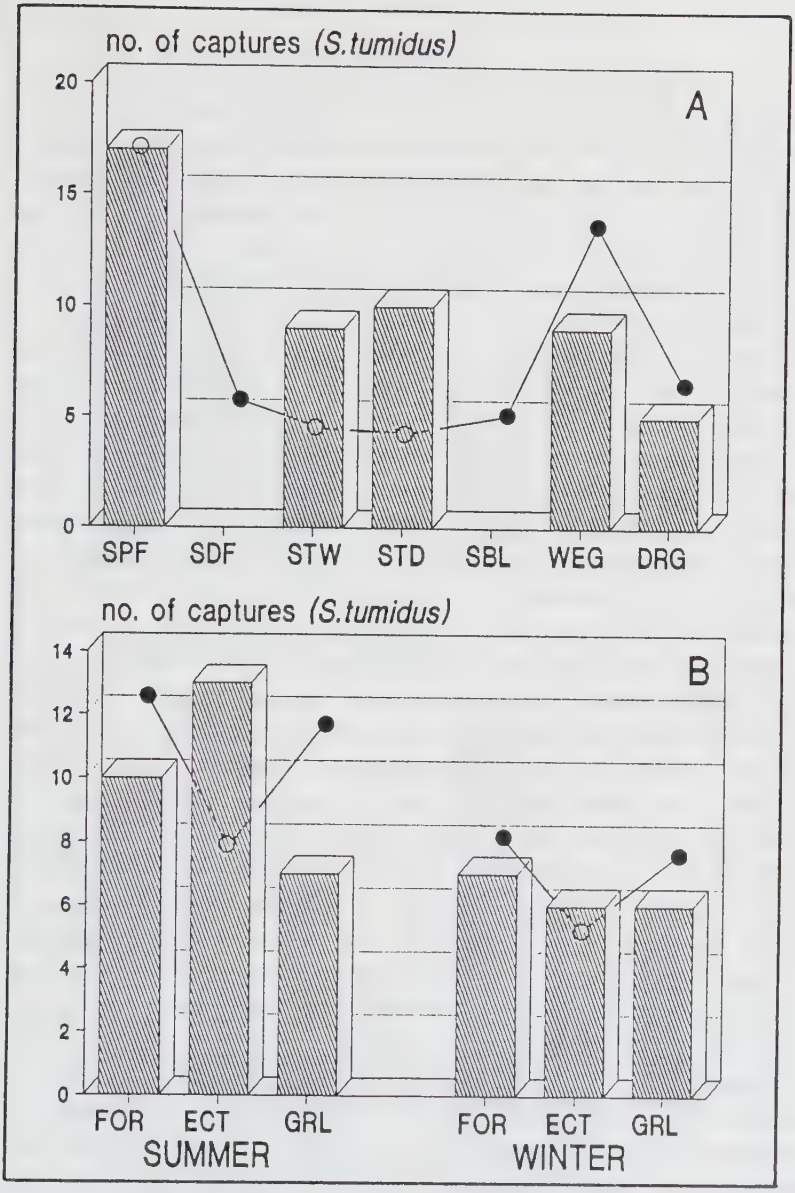


Fig. 21. (A) Observed and expected number of pooled captures from summer and winter for *S. tumidus* in seven habitats (cf. Tab. 7 and 8). The habitat acronyms are from Fig. 20. (B) Observed and expected captures in the three major habitats; forests (FOR), ecotones (ECT), grasslands (GRL) in summer and winter respectively. Observed

Expected

abundant than expected in the transitional wet microhabitats and in the swamp forest, but at least in winter the species appears to use all of them as expected. The total pooled captures of the two seasons showed some restrictions on microhabitat use (G_{adj}=33.63, d.f.=6, P<0.01) (Fig. 21a). The sand forest and the shrubland were strongly avoided.

The increasing niche breadth of *O. delticola* was clearly associated with the number of captures (Tab. 7 and 8). Such association was also observed with the species in a previous work (OLIVEIRA, 1985) in the same area. The captures increased in the swamp forest, suggesting that this is a seasonal microhabitat, and may be associated with a decrease in the dossel use (OLIVEIRA, 1985). *O. delticola* is normally associated with woodlands and forests and exhibits remarkable arboreal ability (LANGGUTH, 1963, BARLOW, 1969, XIMENEZ and LANGGUTH, 1971, OLIVEIRA, 1985). The use of the forest floor and other microhabitats may be associated with the changes in the canopy cover of the semideciduous swamp forest. In the winter the observed and the expected distribution of captures between the microhabitats were at the margin of significance (G_{adj}=12.59, d.f.=6, P=0.05), indicating that the species tried to use all of them proportionally to their availabilities. Despite the seasonal variation, the pooled captures of the two seasons (Fig.22a) showed that the species is able to use all the habitats as expected according to their availability (G_{adj}=10.61, d.f.=6, 0.25>P>0.10). Although the number of captures was low in summer, these were higher in the ecotones, whereas no individual was caught in the forest. In the winter they were higher than expected in the forest and lower in the ecotones and in the grassland. The grassland habitat types were secondary to the species (G_{adj}=9.29, d.f.=2, P<0.01) (Fig. 22b).

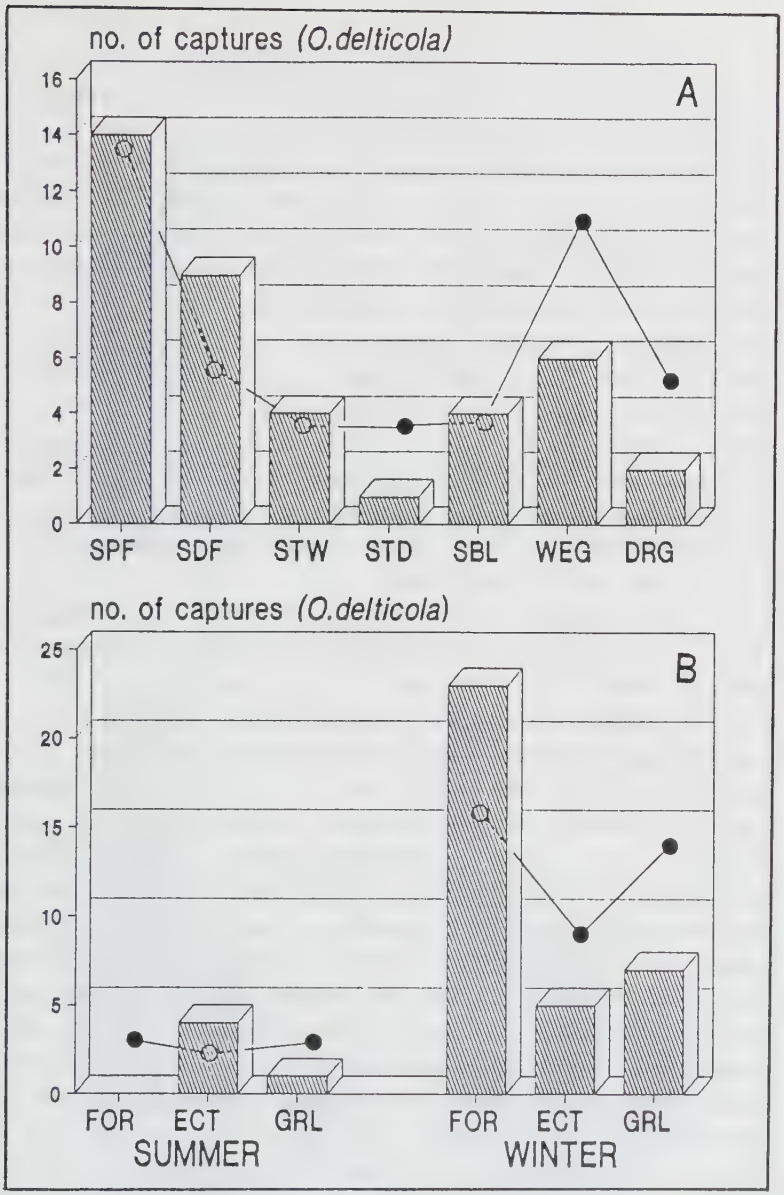


Fig. 22. (A) Observed and expected number of pooled captures from summer and winter for *O. delticola* in seven habitats (cf. Tab. 7 and 8). The habitat acronyms are from Fig. 20. (B) Observed and expected captures in the three major habitats; forests (FOR), ecotones (ECT), grasslands (GRL) in summer and winter respectively. ▨ Observed
O—● Expected

A. serrensis, a species with a wide breadth niche (Fig. 19), was normally associated with the forest and the ecotones (Fig. 23b) (G_{adj}=151.39, G_{adj}=33.67, P<0.001; summer and winter respectively). The grassland was used with restrictions. In the swamp forest and in the swamp forest - dry grassland transitional microhabitats the captures were always more abundant than expected in both the seasons. In the winter, in the sand forest the captures were less abundant than expected, suggesting a low suitability of this microhabitat at least in this season. Only in the dry and in the wet grassland the captures were always less than expected. The pooled captures showed that the species did not use the habitats in the proportions of their availability (G_{adj}=174.12, d.f.=6, P<0.001) (Fig. 23a).

D. kempi presented a relative niche breadth stability (Fig. 19) between the two seasons, and presented some habitat specialization(G_{adj}=11.13, G_{adj}=28.81, d.f.=2, P<0.01; summer and winter respectively) (Fig. 24b). In the summer the captures were greater than expected in the ecotones and in the grassland. In winter the captures increased sharply in the ecotones, remaining at low levels in the forest. The grassland appears to be used in proportion to their relative availability. *D. kempi* was not restricted to wet habitats as in other regions (THOMAS, 1917a, MASSOIA, 1964, BARLOW, 1969) but showed some preferences to those of swampy features. The actual pattern contrasts with previous informations of the region (OLIVEIRA, 1991), suggesting that the spatial disposition of the species has been affected by some factors that may regulate the habitat use. The pooled captures of the two seasons indicated that the species was more frequent than expected in the wet grassland and in the wet transitional microhabitats (G_{adj}=72.67, d.f.=6, P<0.01) (Fig. 24a). The sand forest and the shrubland were strongly avoided.

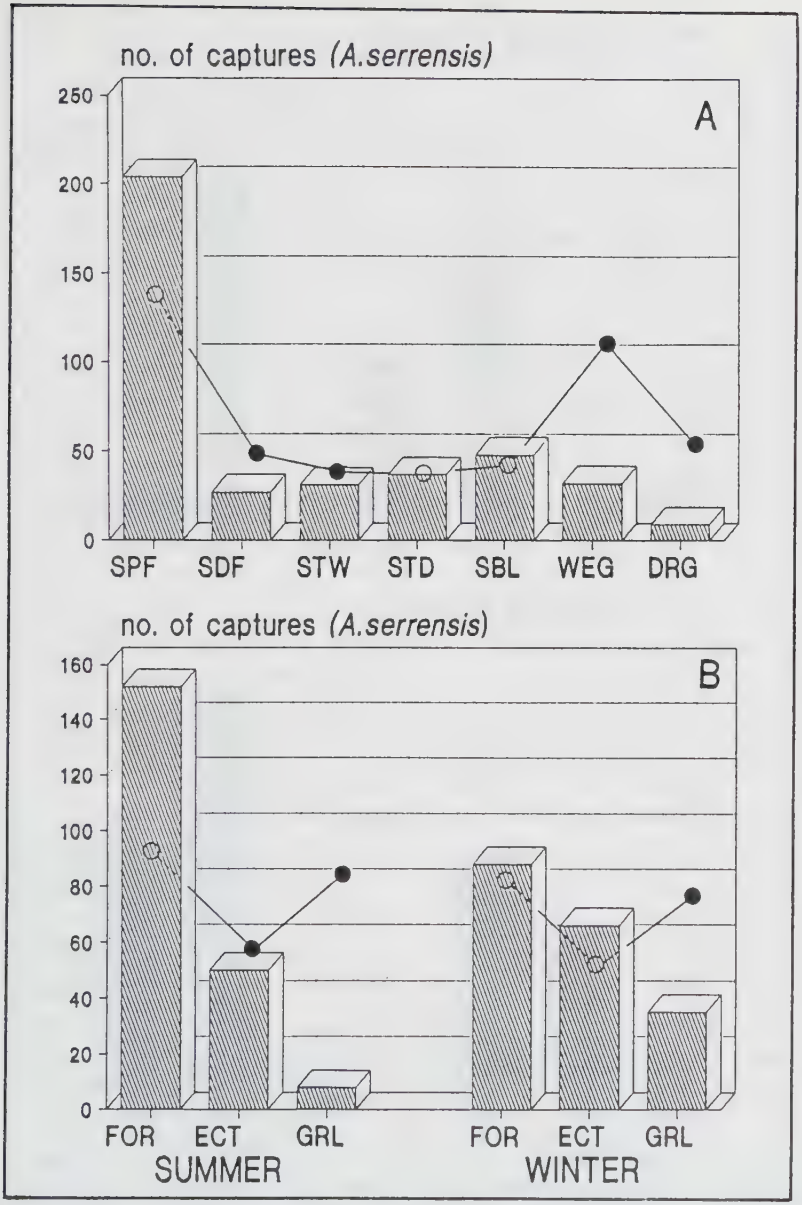


Fig. 23. (A) Observed and expected number of pooled captures from summer and winter for *A. serrensis* in seven habitats (cf. Tab. 7 and 8). The habitat acronyms are from Fig. 20. (B) Observed and expected captures in the three major habitats; forests (FOR), ecotones (ECT), grasslands (GRL) in summer and winter respectively. Observed

Expected

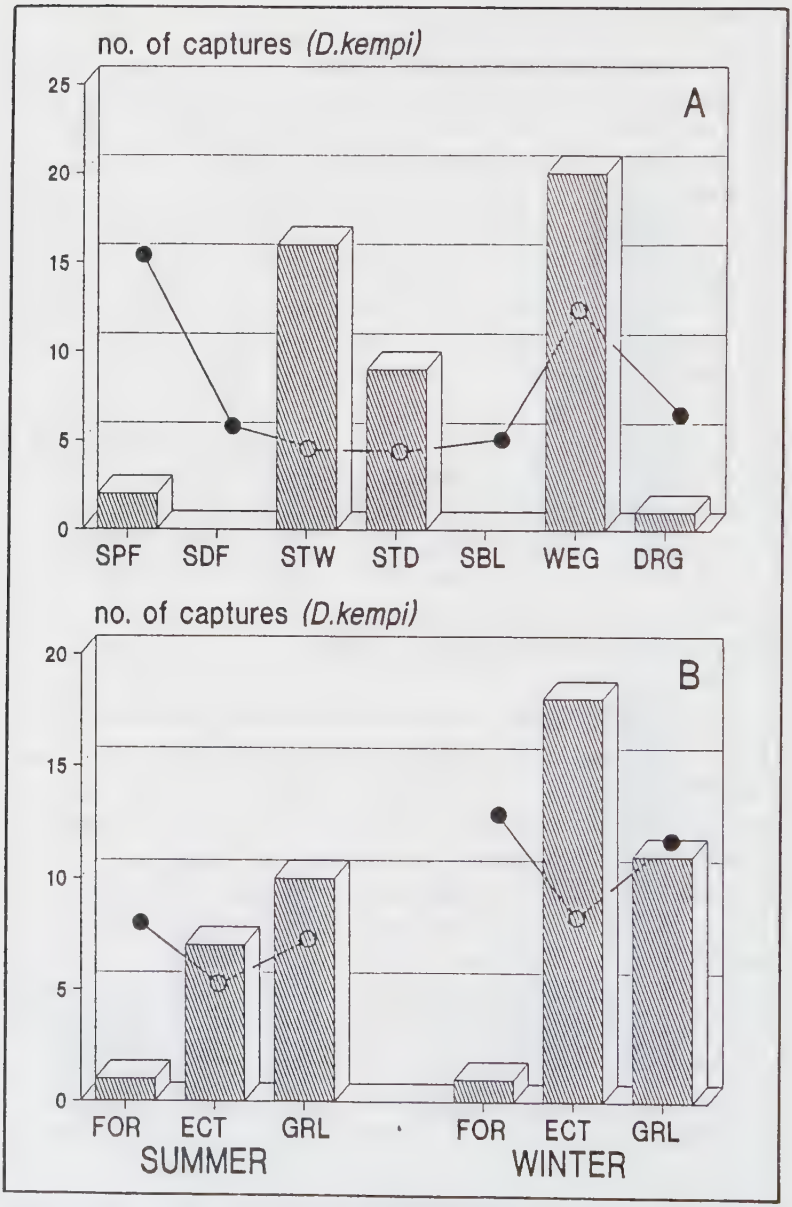


Fig. 24. (A) Observed and expected number of pooled captures from summer and winter for *D. kempi* in seven habitats (cf. Tab. 7 and 8). The habitat acronyms are from Fig. 20. (B) Observed and expected captures in the three major habitats; forests (FOR), ecotones (ECT), grasslands (GRL) in summer and winter respectively. Observed

Expected

The niche breadth of *O. flavescens* presented no variations between the two seasons (Fig. 19). The niche stability contrasted with the dynamic pattern observed on the population in other work (OLIVEIRA, 1991), when the species was very scarce in summer and abundant in winter. The seasonal habitat use normally observed for the species (CONTRERAS and ALVARADO, 1968; CRESPO et. al, 1970; DALBY, 1975) was not evident. In both seasons the captures were normally more abundant than expected in the grassland (Fig. 25b), and less abundant than expected in the ecotones and in the forest, showing a restriction on habitat use (G_{adj}=24.19, G_{adj}=14.10, d.f.=2, P<0.001). The species was always more abundant than expected in the wet and dry grassland. The pooled captures (Fig. 25a) indicate that these are the main habitats. Others are secondary or used with restrictions (G_{adj}=45.31, d.f.=6, P<0.001).

A. azarae presented a relative niche breadth stability between the two seasons, and a slight contraction in winter when the captures were more abundant (Fig. 19). The species has been found in several habitat types ranging from agrosystems (DE VILLAFAÑE et al., 1973; KRAVETZ and DE VILLAFANE, 1981) dry grasslands (PEARSON, 1967; BARLOW, 1969), woodlands and forests (BARLOW, 1969; OLIVEIRA, 1985), to overflowed or dry places in marshes (BARLOW, 1969, XIMENEZ and LANGGUTH, 1971). *A. azarae* was notoriously associated with grassland and ecotones (G_{adj}=33.26, d.f.=2, P<0.01) (Fig. 26b), contrasting with other data obtained in the same region (OLIVEIRA, 1985), when the species was frequent in the sand forest. The data from winter, when the captures were more abundant, showed a positive selection to the shrubland and the dry grassland and an avoidance to the forest habitat types (G_{adj}=70.51, d.f.=6, P<0.001). The wet grassland was used but with some restrictions. The same pattern was observed

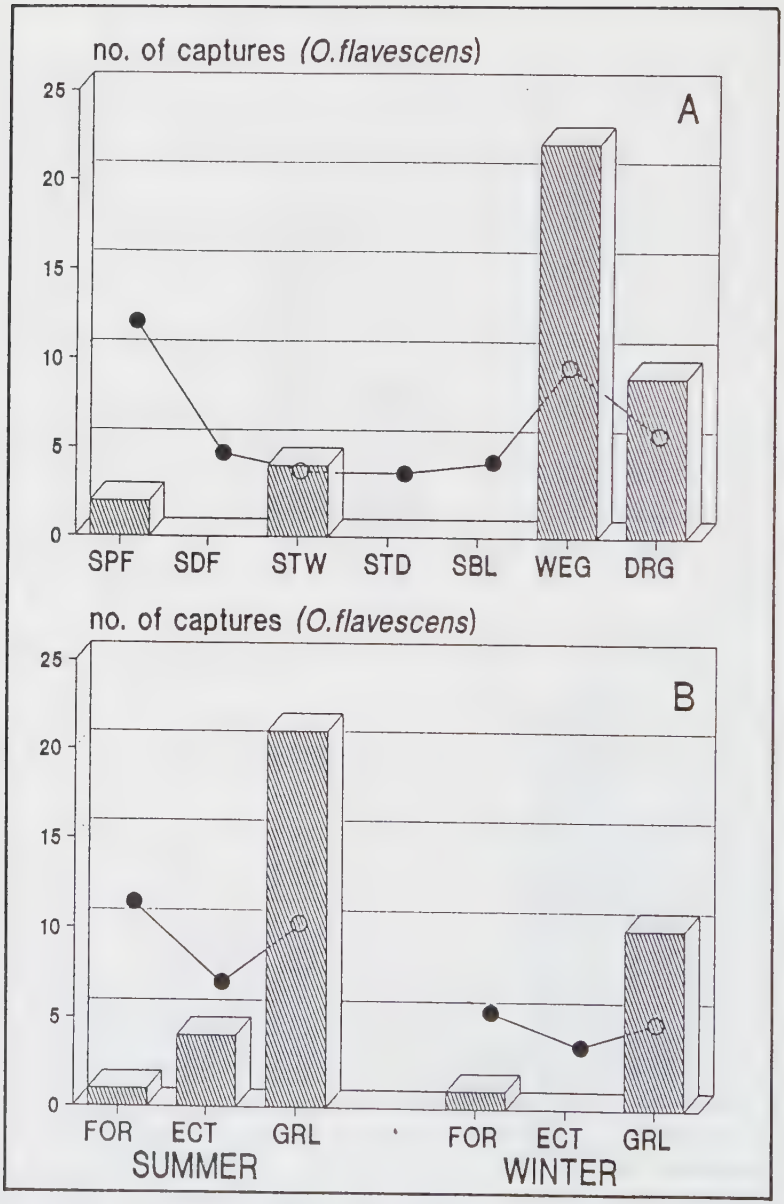


Fig. 25. (A) Observed and expected number of pooled captures from summer and winter for *O. flavescens* in seven habitats (cf. Tab. 7 and 8). The habitat acronyms are from Fig. 20. (B) Observed and expected captures in the three major habitats; forests (FOR), ecotones (ECT), grasslands (GRL) in summer and winter respectively. ▨ Observed
O—● Expected

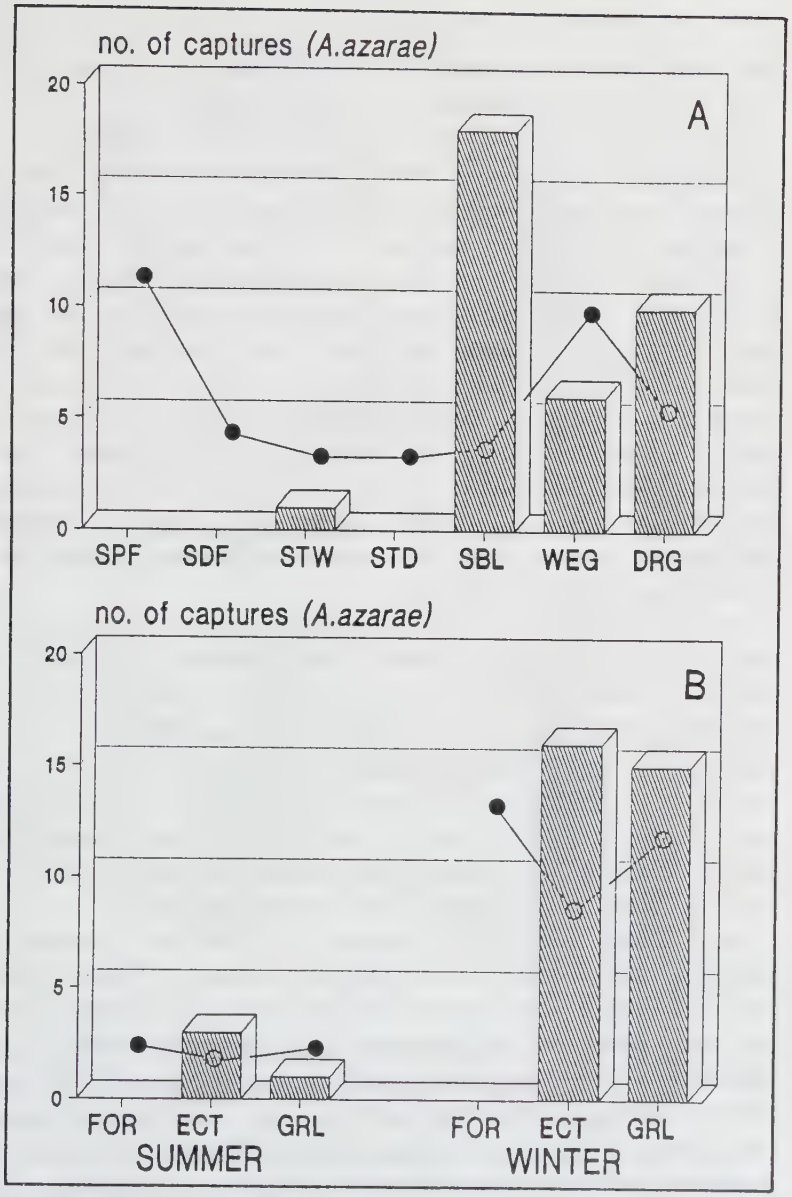


Fig. 26. (A) Observed and expected number of pooled captures from summer and winter for *A. azarae* in seven habitats (cf. Tab. 7 and 8). The habitat acronyms are from Fig. 20. (B) Observed and expected captures in the three major habitats; forests (FOR), ecotones (ECT), grasslands (GRL) in summer and winter respectively. ▨ Observed
O—● Expected

when pooling the summer and winter captures (G_{adj}=73.34, d.f.=6, P<0.01) (Fig. 26a).

O. rufus presented the narrowest niche breadth in the community (Fig. 19). A small variation was observed in winter when the species was trapped only in the dry grassland, its main habitat. In the swamp forest-dry grassland ecotones, individuals were caught only in summer (Fig. 27b). Certainly this and the sand forest edge (OLIVEIRA, 1991) were the main microhabitat for the species before removing the cattle. It was rare in wet areas and certainly the occurrence normally observed in such microhabitat type in other regions (SANBORN, 1929; BARLOW, 1969) may partially be a result of habitat erosion by livestock grazing. In the overgrazed adjacent area the species was absent. All the other microhabitat types were strongly avoided (Fig. 27a).

H. brasiliensis was caught only in the dry grassland, which certainly is a secondary microhabitat. Although the species presents semiaquatic features (HERSHKOVITZ, 1955; SIERRA DE SORIANO, 1965; MILLER and ANDERSON, 1977), is able to use several dry unforested habitat types. In the region it is abundant in grassy swamps with *Z. bonariensis* and *S. californicus*, and in lagoons and canal banks. The single capture in winter may be an evidence that the species inhabits the area with low density.

C. laucha was only caught in heavily overgrazed pastures (OLIVEIRA, 1991) and at burrows in sand dunes near the coast. The species shows a high ability to live in agrosystem and in overgrazed pastures (BARLOW, 1969; VALLEJO and GUDYNAS, 1981; KRAVETZ and DE VILLAFAÑE, 1981; KRAVETZ et al., 1981; DE VILLAFAÑE et al., 1988; BUSCH et al., 1984). The occurrence in an uninhabited and less suitable habitats to other species, may reflect a competitive exclusion or a habitat avoidance, since the dry grassland has a dense herb layer that contrasts with

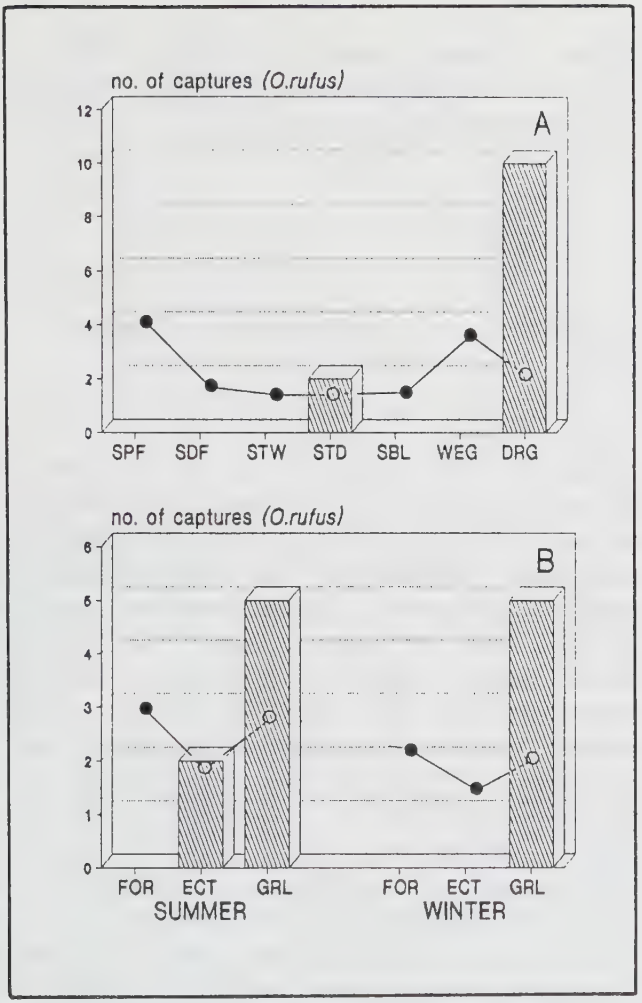


Fig. 27. (A) Observed and expected number of pooled captures from summer and winter for *O. rufus* in seven habitats (cf. Tab. 7 and 8). The habitat acronyms are from Fig. 20. (B) Observed and expected captures in the three major habitats; forests (FOR), ecotones (ECT), grasslands (GRL) in summer and winter respectively. ▨ Observed
O—● Expected

the overgrazed adjacent areas (OLIVEIRA, 1991). The ability to use burrows as shelters and nests, facilitates the survival in overgrazed pastures.

2.1.4. SPECIES / HABITAT STRUCTURE RELATIONSHIPS

In a bivariate correlation analysis with the mean values of the structural variables *per* habitat no significant correlation with the number of rodent species caught (NSC) was obtained for the winter data (all $P>0.10$). The pooled captures of both seasons showed that the increasing number of species caught is related to foliage height density and to the herb layer height ($P<0.05$) (Fig. 28, Fig. 29). Both variables, related to vertical habitat structure, vary along the primary and the secondary gradients. Those habitats with low herb layer and low foliage height density appear to be more extreme to the community as a whole.

The habitats can be described by a complex of many variables that affect differently the species, and explain the major trends along the gradients. Among the seventeen measured variables, nine of them (HCV, LIT, FLOOD, SHRUB, TDIS, TDIA, BRUNCH, FHD25, and FHD50) fit very well to the species data ($P<0.05$) for the winter survey (Tab. 4). For the analysis pooling the captures from summer and winter, and excluding the four variables more subjected to the seasonal variations (CANCV, LIT, MUD, and FLOOD), almost the same set was obtained (Tab. 9); only herbaceous height (HHT) was added to the set. They contribute significantly

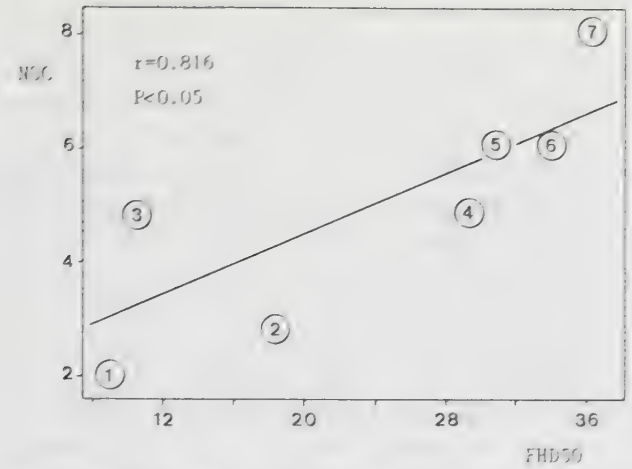


Fig. 28. Relationships between the number of species caught (NSC) (summer and winter pooled captures, cf. Tab. 7 and 8) and foliage height density from 2.5 to 50 cm (FHD50) in seven habitat types. 1. sand forest; 2. shrubland; 3. swamp forest; 4. wet grassland; 5. swamp forest - dry grassland ecotone; 6. swamp forest - wet grassland ecotone; 7. dry grassland.

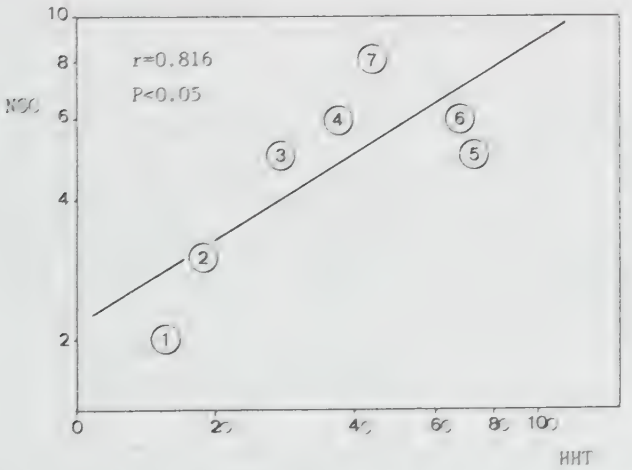


Fig. 29. Relationships between the number of species caught (NSC) (summer and winter pooled captures, cf. Tab. 7 and 8) and mean herbaceous height (HHT) in seven habitat types. The habitat numbers are from Fig. 28.

	Canonical coefficients				Correlation coefficients			
AXIS	1	2	3	4	1	2	3	4
variable								
HHT*	-0.03	0.05	0.02	-0.04	-0.23	0.54	0.09	0.0
HCV*	0.02	0.01	0.06	0.02	-0.63	0.08	0.18	0.0
FHD25*	-0.09	-0.07	-0.02	0.08	-0.69	0.24	0.07	0.0
FHD50*	0.08	1.31	0.08	-0.07	-0.61	0.35	0.09	-0.1
FHD100	-0.05	-0.06	-1.22	-0.10	-0.48	0.40	0.08	-0.1
FHD170	0.04	0.01	0.08	0.05	-0.31	0.41	0.12	-0.0
CANHT	0.01	-0.05	0.02	-0.00	0.70	-0.05	0.11	0.0
TDIA*	0.05	0.02	-0.02	0.01	0.62	0.00	0.05	0.0
TDIS*	0.05	0.04	-0.01	0.01	0.63	0.16	0.01	0.0
BRANCH*	-0.02	0.00	0.06	-0.02	0.60	-0.02	0.19	-0.0
FLOG	0.00	-0.01	0.01	-0.01	0.28	-0.08	0.07	-0.0
SHRUB*	0.02	0.02	0.01	0.00	0.39	0.28	-0.09	0.0
ROHIHO	0.00	0.02	0.02	0.00	0.46	-0.02	-0.09	0.0

Table 9. Canonical coeficients and intra-set correlations of environmental variables with the first four axis of canonical correspondence analysis (CCA) (summer and winter captures pooled). The environmental variables were standardized to unit variance after log-transformation. Variable acronyms are from Tab. 1. * = variables with t-value <0.05.

to the multiple regression performed by the Canonical Correspondence Analysis (JONGMAN et al., 1987) and constitute a subset of environmental variables that explain equally well as the full set (TER BRAAK, 1987a) the species-environment biplot. The herbaceous cover (HCV) showed extreme variations between the habitats and contributes largely to explain the species distribution ($t=2.18$, $t=2.89$, $P<0,05$; summer and winter respectively). Some species select positively or avoid habitats with extreme values, showing that the herbaceous layer cover plays an important role on the composition and density of the rodent assemblages. The variables tree dispersion (TDIS) and tree mean trunk diameter (TDIA), more related to forest sites, are negatively correlated to the herb layer features (APPENDIX 2). This suggests that the rodent's distribution can be explained by an inter-habitat variation. The variable SHRUB is difficult to relate to the rodent species but characterizes specially edge habitats with high small trees density. This variable co-varies significantly with herbaceous cover ($r=-0.421$, $d.f.=61$, $P<0.001$), relative importance of mud ($r=0.460$, $d.f.=61$, $P<0.001$), canopy cover ($r=0.290$, $d.f.=61$, $P<0.05$), and other variables that characterize the habitats (APPENDIX 2). The species occurrence and density certainly do not depend only on the best variable or on the set selected by the regression. The correlations among them and the remaining variables, and their meaning for the habitats related to rodents, suggest a good approach when taken together. Some variables can be complementary in explanatory power (WHITTAKER, 1984) regarding the habitats and the gradient complexity.

The first and the second axis of the CCA accounted for 63.72% of the main variation observed in winter (Tab. 10) and 74.42% to the pooled captures data respectively (Tab.

11). The first eigenvalues (λ_1=0.34, λ_1=0.32; winter and the pooled data respectively) were significant (MCptλ_1, P=0.01) and show high relation between the rodent species and the environmental variables. Figures 30 and 31 display the ordination diagram of the species and environmental scores on axis 1 and 2. The first axis on Fig. 30(λ_1=0.34) separates the species more related to grassland and forest habitats. The second axis (λ_2=0.28) is seen to separate the species more related to dry sites from those with optima in the wet sites. The degree of similarity between the species (d_{jk}) in relation to the environmental variables that describe the gradients revealed three groups resulting from the cluster analysis of the distance matrix of the species CCA scores (Tab. 12). *O. rufus* and *A. azarae* in the lower left corner of the diagram, showed negative correlation with MUD and FLOOD. Their optima (species centroids) lie in dry grasslands sites with high ground cover and high foliage height density up to 25 cm high.

	AXIS			
	1	2	3	4
Eigenvalue	0.34	0.28	0.17	0.09
% Var. acc. for	34.78	28.94	17.74	8.76
Cum. % var. acc.	34.78	63.72	81.46	90.22

Table 10. Taim region (winter data). Eigenvalue, percentage of total variance, and cumulative percentage attributable to each axis in the Canonical Correspondence Analysis (CCA).

	AXIS			
	1	2	3	4
Eigenvalue	0.32	0.16	0.08	0.06
% Var. acc. for	48.69	26.73	11.55	8.97
Cum. % var. acc.	48.69	74.42	86.97	95.94

Table 11. Taim region (summer and winter pooled data). Eigenvalue, percentage of total variance, and cumulative percentage attributable to each axis in the Canonical Correspondence Analysis (CCA).

	AXIS			
	1	2	3	4
O rufus	-2.02	-0.29	-0.58	-3.10
D. kempi	0.06	2.06	1.00	-0.12
A. azarae	-2.38	-0.33	-0.29	0.69
A. serrensis	0.50	-0.19	-0.41	0.05
S. tumidus	0.36	0.87	-0.74	0.00
O. flavescens	-1.28	0.38	0.65	0.42
O. delticola	0.35	-1.21	1.28	-0.11

Table 12. Species scores on four ordination Canonical Correspondence Analysis (CCA) axis for the Taim winter data.

O. flavescens is related to grassland but the species centroid lies on more wet sites than *O. rufus* and *A.*

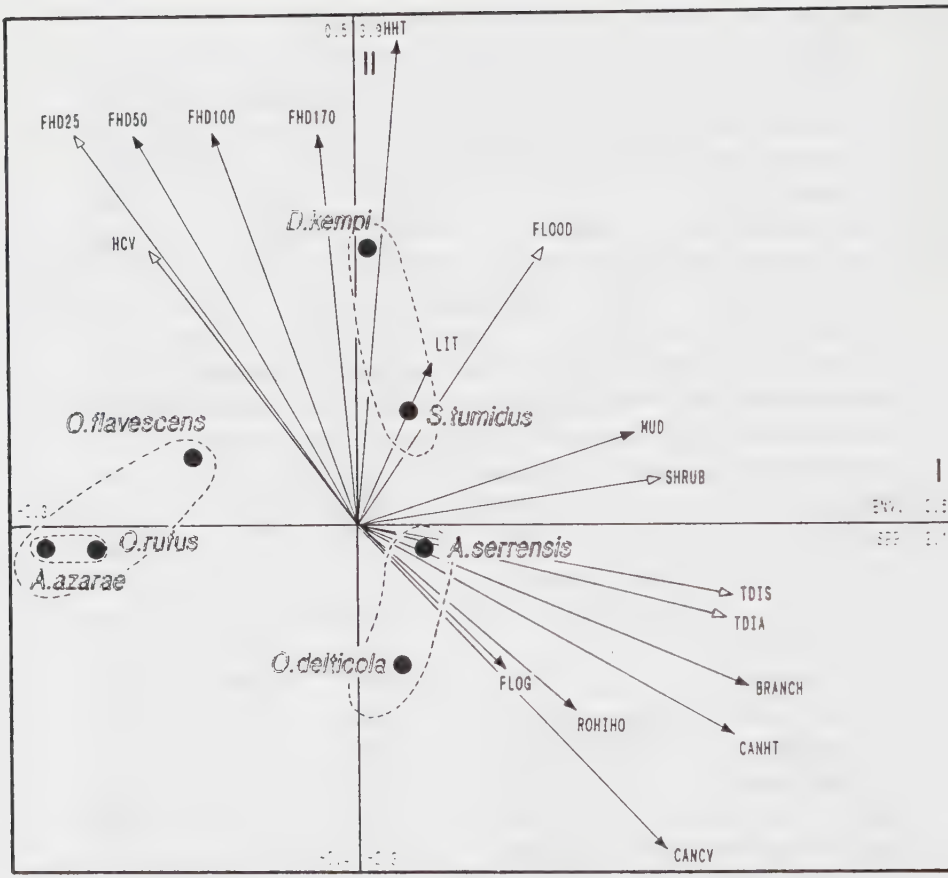


Fig. 30. Ordination diagram (winter captures) based on Canonical Correspondence Analysis (CCA) of the rodent species data with respect to microhabitat structure (for total species caught see Tab. 8). The dotted lines delimit the three groups whose Euclidean distance between the centroids is less than $\bar{d}_{jk}$ of CCA scores. The open arrows are the variables that explains the species data almost equally well as the full set (t-value <0.05). The environmental variable acronyms are from Tab. 1.

azarae. The species in the upper right corner of the diagram - *D. kempi* and *S. tumidus* - are more related to wet habitats with high HHT, FLOOD, or MUD, and SHRUB. *D. kempi* occurs in habitats with well developed herbaceous layer. The species distribution is highly correlated with herbaceous height and with the foliage height density up to 170 cm high. The wet grassland appears to be the best habitat for the species. *S. tumidus* seems to avoid dry sites. The species centroid is more related to those variables that describe wet transitional habitats between forest and grassland, and with the swamp forest. *O. delticola* showed a negative correlation with all the variables that describe herb layer features. The species is related to open sites of the forest floor with low herb layer and low foliage height density, and high canopy cover (CANCOV), high fallen logs importance (FLOG), and with high importance of potential hiding holes (ROHIHO). The species tends to select dry sites in woody habitats. *A. serrensis*, the more centered species in the diagram showed the lowest weighted average with respect to the environmental variables. This means that the species is less related to the gradients and its relations to the variables are not precise. The high frequency of captures of *A. serrensis* along the transects agrees with the CCA results and permits only the inference that the species centroid lies in the forest.

The analysis by pooling the summer and winter captures (Fig. 31) but without the variables CANCV, LIT, MUD, and FLOOD, more seasonal-dependents, once more disclosed three species groups (Tab. 13) and a more general pattern. *O. flavescens* and *A. azarae* are grouped together. They are related to sites with high ground cover but normally with low herbaceous height and low foliage height density. The group related to sites with high foliage height density is heterogeneous and includes three species: *S. tumidus*, that

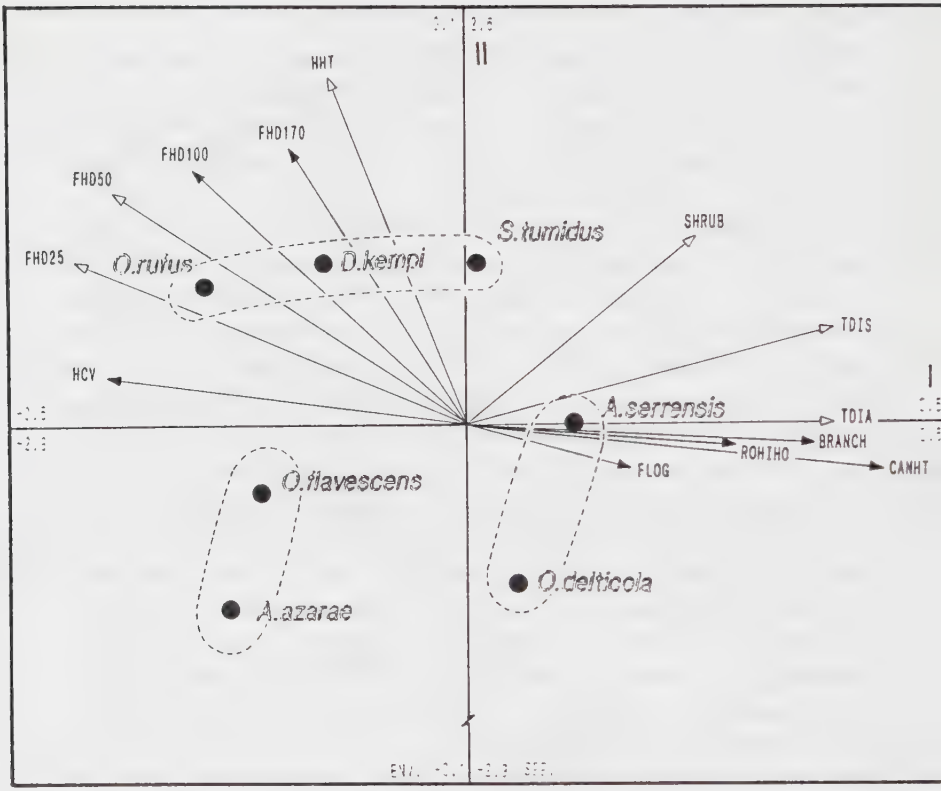


Fig. 31. Ordination diagram (pooling summer and winter captures) based on Canonical Correspondence Analysis (CCA) of the rodent species data with respect to microhabitat structure (for total species caught see Tab. 7 and 8). The dotted lines delimit the three groups whose Euclidean distance between the centroids is less than $\bar{d}_{jk}$ of CCA scores. The open arrows are the variables that explains the species data almost equally well as the full set (t-value <0.05). The environmental variable acronyms are from Tab. 1.

presents the lowest correlation with the herb layer features; *D. kempi*, that shows high correlation with foliage height density up to 100-170 cm high; and *O. rufus* that shows the highest negative correlation with the variables set that characterizes the woody sites. *A. serrensis* lies near the centre of the diagram and is less related to the gradients described. However, this species showed some relations with the variables set that describes the forest features. *O. delticola* showed the same relations to sites with low herbaceous height and low foliage height density as in the winter analysis.

	AXIS			
	1	2	3	4
O rufus	-1.78	0.83	-0.18	-2.44
D. kempi	-0.97	1.07	0.80	0.45
A. azarae	-1.60	-1.20	-1.08	0.20
A. serrensis	0.73	-0.06	-0.11	0.05
S. tumidus	0.08	1.04	-0.53	-0.04
O. flavescens	-1.40	-0.42	0.36	0.51
O. delticola	0.32	-1.10	0.99	-0.54

Table. 13 Species scores on four ordination axis of Canonical Correspondence Analysis (CCA) for summer and winter pooled data (Taim).

There are evidences that the rodent species react to sudden differences in the habitat structures. A great part of the variation on captures may be explained on a microhabitat scale. The variation on the captures was closely related to the vegetation zones. These zones are partially delimitated by the inactive cliff that separates

the sandy and the lagoonal terraces (Fig. 4) where the two types of forests, grasslands, and their respectives ecotones are adjacents.

The partial Canonical Correspondence Analysis for the winter data, carried out with the variables related to the "drain conditions" (FLOOD and MUD) as covariables, was significant ($MCpt\,\lambda_1$, $P=0.02$). Thus, the remaining variables are sufficient to explain the species distribution. The habitats' differences related to swampy features were insufficient to explain the rodent distribution along the gradients. The variation in the captures that remained after fitting the variables related to herb layer (HHT, HCV, FHD25, FHD50, FHD100, and FHD170) as covariables, was not significant ($MCpt\lambda_1$, $P=0.07$). This means that this set alone can explain the observed differences in the captures between the microhabitats. The herb layer features present its maximal expression in the grassland and in the transitional microhabitats. The lowest values were observed in the swamp forest but this variables set was always negatively related (APPENDIX. 2) to those that characterized forest habitats (e.g. $r_{HCV,CANCV}=-0.806$; $r_{FHD25,CANCV}=-0.751$; $r_{FHD25,CANHT}=-0.649$). These two extremes of the main gradient clearly demonstrate the habitat ranges that regulate the rodent assemblages' features.

The description of all the positive trap sites along the two line transects that intercepted the vegetation zones, allowed their classification to be based on the sample scores derived from the environmental variables in relation to the axis of the CCA ordination. The first axis ($\lambda=0.34$) explained 34.78% of the variation in original data (Tab. 10) and had a high positive correlation with the variables set (Tab. 4) that characterized the forest sites, such as canopy cover, canopy height, mean trees trunk diameter, and tree dispersion index. Furthermore,

this axis presents a negative correlation with some variables that describe the herb layer features (FHD25, FHD50, and HCV). Thus, it can be interpreted as a forest to grassland gradient, whereas, at the same time it characterizes the study area in a microhabitat scale. The continuous curve of the CCA scores along the first trapline (Fig. 32.a) showed that the trap stations in the north and in the south extremes of the transect are close together regarding their structure, even if they are separated by the inactive cliff that limits the sandy and the lagoonal terraces. The ordination of the trap stations by the sample scores derived from the species scores (Fig. 32.b) showed a close agreement between the two diagrams ($r_{s1,e1}$=0.722, n=22, P<0.001). This is an evidence that the observed variation in the rodent captures (52.13%) is conditioned by the microhabitat structure. Even if different, the sandy and the swamp forests are similar regarding the rodents. Thus the forest microhabitats are more fine-grained (LEVINS, 1968) and the environment appears to be essentially uniform to the assemblage when compared to the grassland habitat types. However, the variations between the trap sites are coarse-grained regarding some habitat types especially when forest and grassland are compared.

The second trapline was more variable than the first one (Fig. 33.a) regarding the variations between the traping sites. However, this is at least partly due to the fact that the trapline intercepted not only a small area of the swamp forest (Fig. 4), but also more wide forest-grassland ecotones with dense herb layer. The ordination of the trap stations by the sample scores derived from the species scores (Fig. 33.b) showed a significant covariation between the species and environmental variables ($r_{s2,e2}$=0.686, n=34, P<0.001). The lower influence of the environmental variables on the rodent assemblage (47.06%)

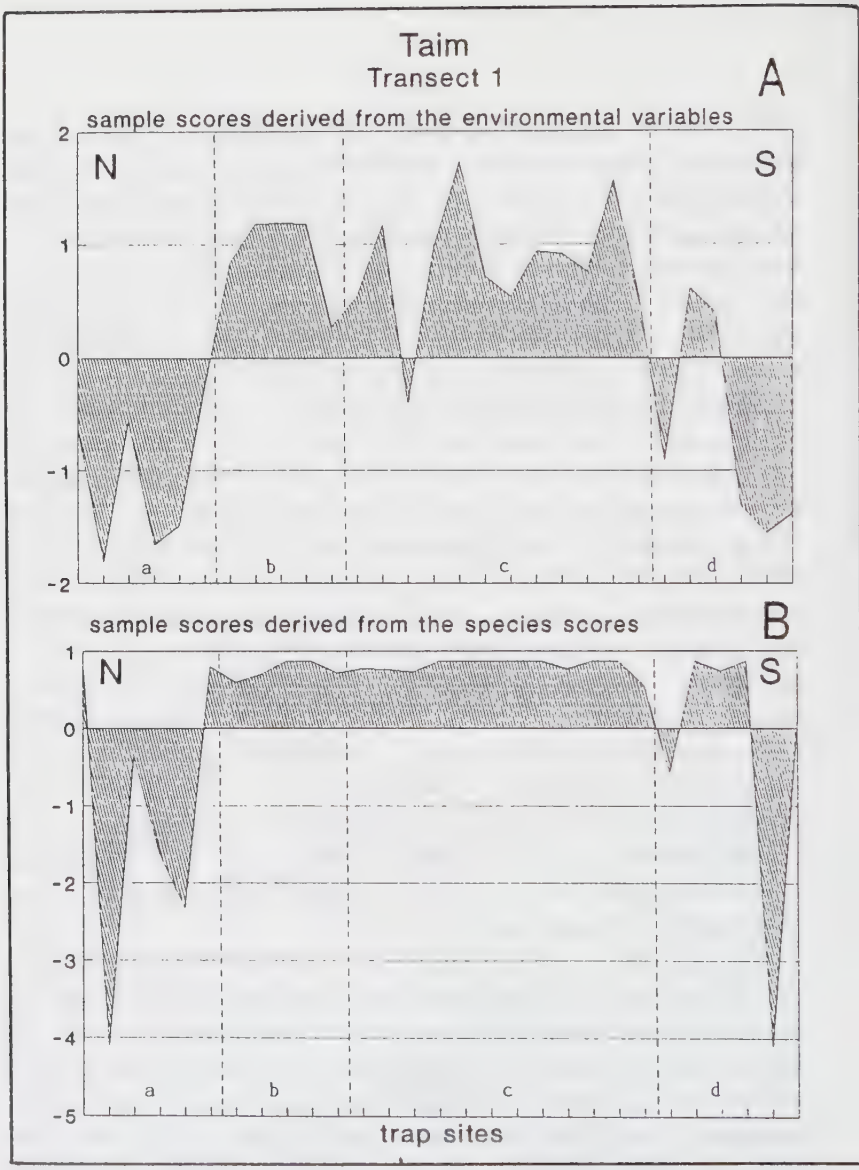


Fig. 32. Distribution of CCA first axis scores which are linear combination of environmental variables (A) and species scores (B) along the transect 1 for the winter data. Transect line conform Fig. 4. a. shrubland, b. sand forest, c. swamp forest, d. wet grassland. N = North. S= South.

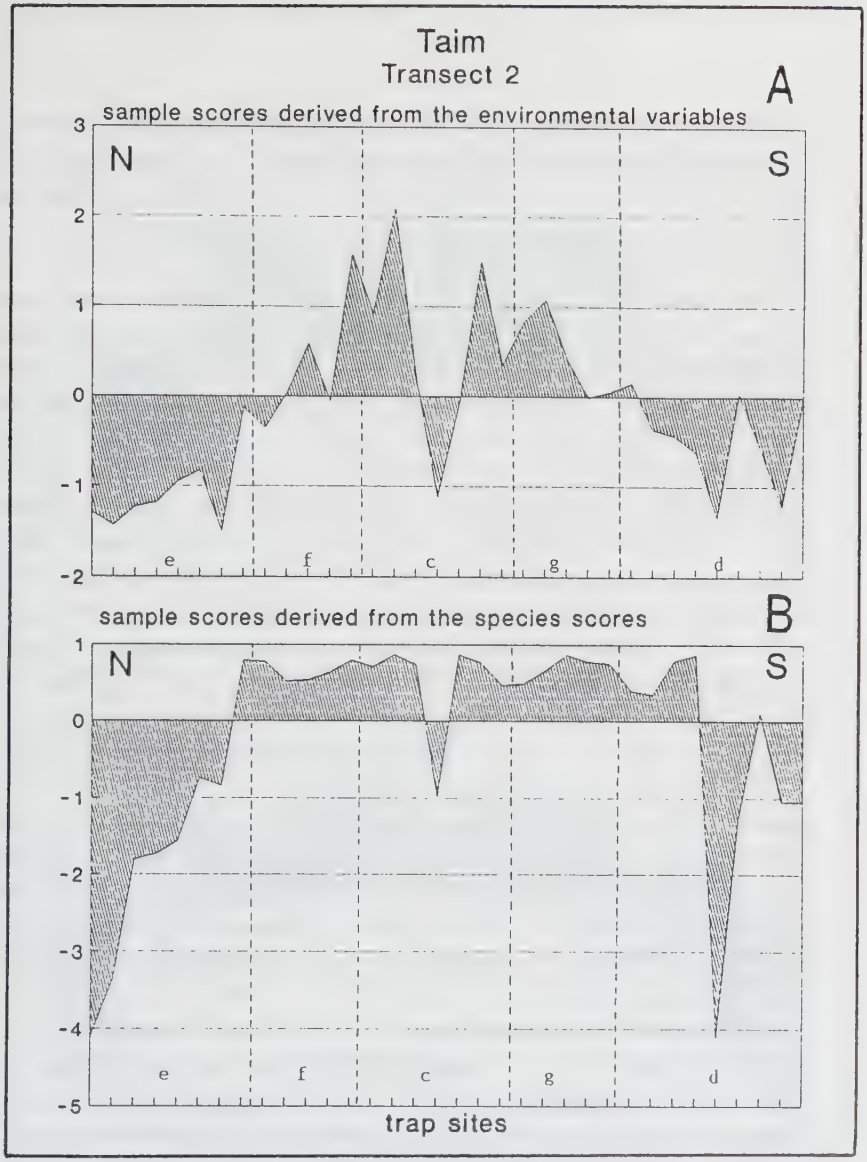


Fig. 33. Distribution of CCA first axis scores which are linear combination of environmental variables (A) and species scores (B) along the transect 2 for the winter data. Transect line conform Fig. 4. c. swamp forest; d. wet grassland; e. dry grassland; f. swamp forest - dry grassland ecotone; g. swamp forest - wet grassland ecotone; N = North, S = South.

along this trapline is partially due to the greater relative importance of ecotones that are used by the grassland and forest species, and to the increasing frequency of forest elements (*A. serrensis* and *O. delticola*) in the grasslands.

The analysis by pooling the summer and winter captures (Fig. 34 and Fig. 35), excluding the variables more seasonal-dependents as CANCV, LIT, MUD, and FLOOD, showed a more general pattern since the seasonal variations in the captures were included. The first axis (λ=0.32) explained 48.69% of the variation in original data (Tab. 11) and had a high positive correlation with the variables set that characterized the forest sites (Tab. 9). Furthermore, it presented a negative correlation with the set more related to the grassland habitat types (HHT, HCV and FHD25 to FHD170). Thus, the two major habitat types (forest and grassland) presented opposing trends. A significant correlation was observed between the rodent captures and the microhabitat structure ($r_{s1,e1}$=0.862, n=35; $r_{s2,e2}$=0.809, n=34; P<0.001) in both trap-lines. The lower influence of the environmental variables on the rodent captures, in the second trapline (65.45%), may be partially due to the more gradual variation within the vegetation zones, allowing the increase of captures in part by chance. Furthermore, the expansion of species normally related to forest (*A. serrensis* and *O. delticola*), over grasslands, is the main cause of the observed pattern. The sandy forest and the shrubland in the first trapline limited the occurence of several rodents (e.g. *O. rufus*, *D. kempi*, *S. tumidus*), thus increasing the predictability of captures based on the microhabitat structure.

The second axis regarding the winter data (λ=0.28) had a high positive correlation with the herb layer variables (HHT, HCV, and FHD25 to FHD170) and the relative

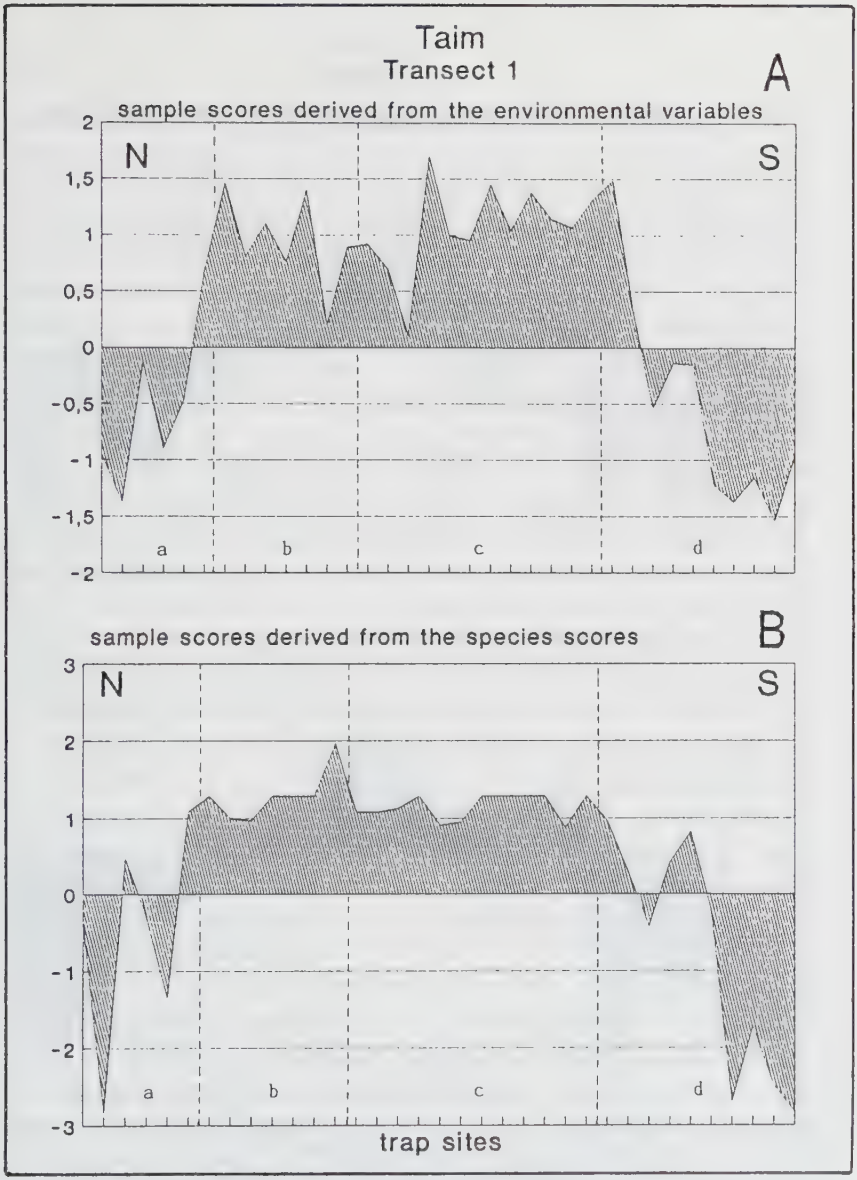


Fig. 34. Distribution of CCA first axis scores which are linear combination of environmental variables (A) and species scores (B) along the transect 1 for the summer and winter pooled captures. Transect line conform Fig. 4. a. shrubland, b. sand forest, c. swamp forest, d. wet grassland. N = North. S= South.

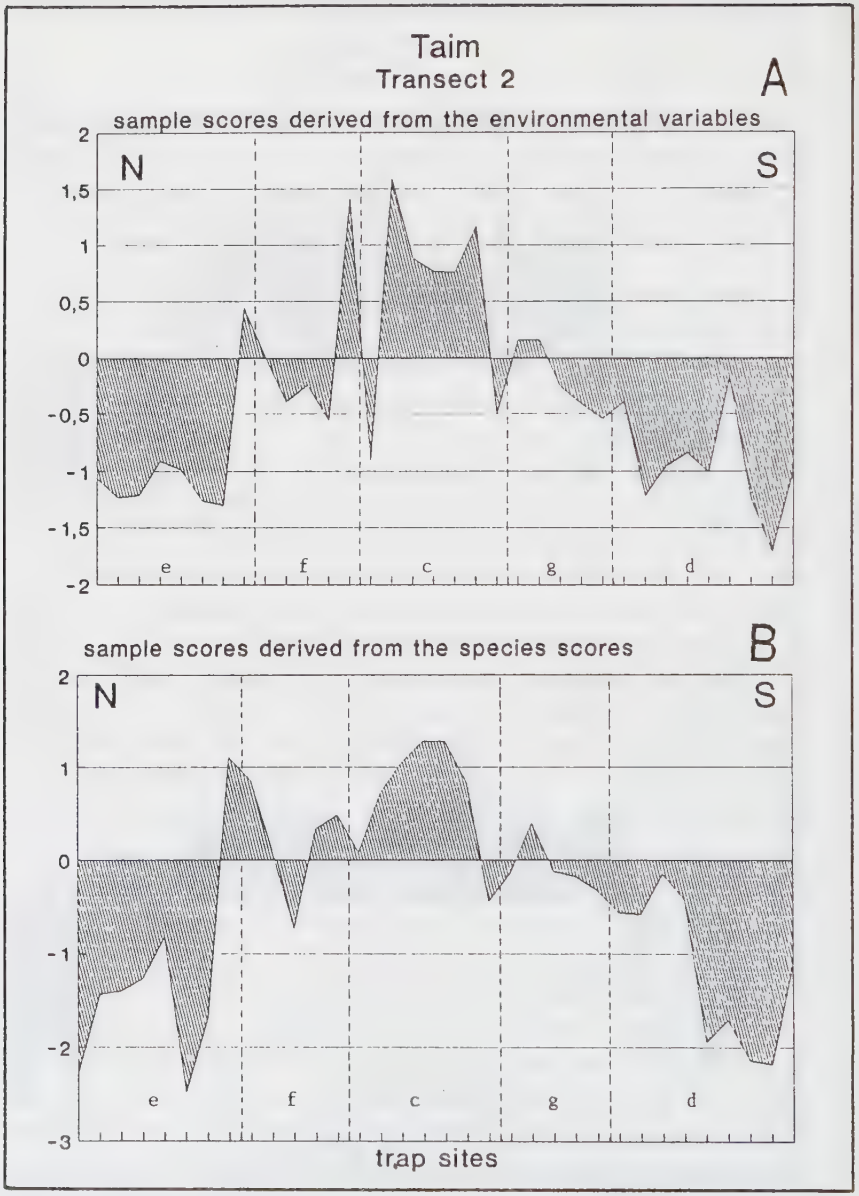


Fig. 35. Distribution of CCA first axis scores which are linear combination of environmental variables (A) and species scores (B) along the transect 2 for the summer and winter pooled captures. Transect line conform Fig. 4. c. swamp forest, d. wet grassland, e. dry grassland, f. swamp forest - dry grassland ecotone, g. swamp forest - wet grassland ecotone. N = North. S= South.

importance of floods (FLOOD). This axis was negatively correlated with canopy cover (CANCV) and with other variables related to the forest structure (Tab. 4). It represents particularly the variations within grasslands, clearings, and ecotones, and explains 28.94% of the the original data. As showed in the diagram (Fig. 36), the structure and composition of the rodent assemblage is mainly determined by the microhabitat features, such as the herb layer variables at the trap sites on the lagoonal terrace ($r_{s1,e1}$=0.633, n=29; $r_{s2,e2}$=0.762, P<0.01; first and second transect lines respectively). The wet ecotones in the second transect line are structured as the wet grasslands (Fig. 36.c). Likewise, the rodent assemblages are in accordance with their features (Fig. 36.d). In the first transect line an extensive area (Fig. 36.b) presented a rodent assemblage compositition contrasting with the previous one. The species more related to wet grasslands or transitional microhabitats, as *D. kempi*, *O. flavescens*, and *S. tumidus*, are rare or absent. Only in the extreme south of the transect line the rodent captures resembled a wet grassland rodent community. Clearings in the swamp forest sites, with more dense ground layer, were similar to wet grassland regarding the habitat structure. Thus, species related to wet grasslands were also favoured in that microhabitats.

The correlations between the first CCA axis derived from the species scores and the first axis of the samples scores, which are linear combinations of environmental variables (i.e. species-environment correlations, TER BRAAK, 1987a; JONGMAN et al., 1987), were significant ($r_{s1,e1}$=0.707, n=63; $r_{s1,e1}$=0.855, n=69; P<0.001, winter and pooled data respectively) (Fig. 37). The microhabitat structure variables related to the first axis accounted for the main variation observed in the distribution of captures related to the same axis for the winter (50.02%)

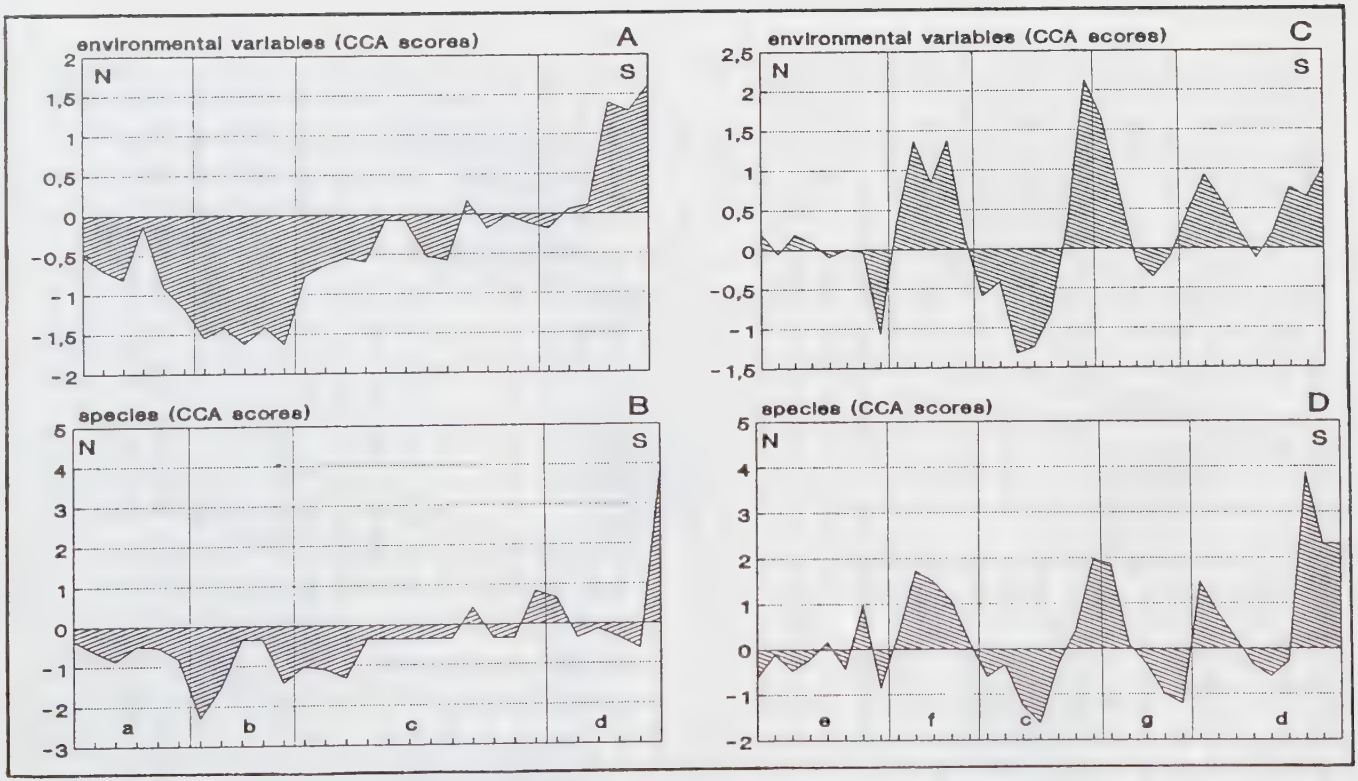


Fig. 36. Distribution of CCA axis 2 scores which are linear combination of environmental variables and species scores along the first (A and B) and the second transect (C and D) for the winter data. Transect lines conform Fig.4. a. shrubland, b. sand forest, c. swamp forest, d. wet grassland, e. dry grassland, f. swamp forest - dry grassland ecotone, g. swamp forest - wet grassland ecotone. N = North, S = South.

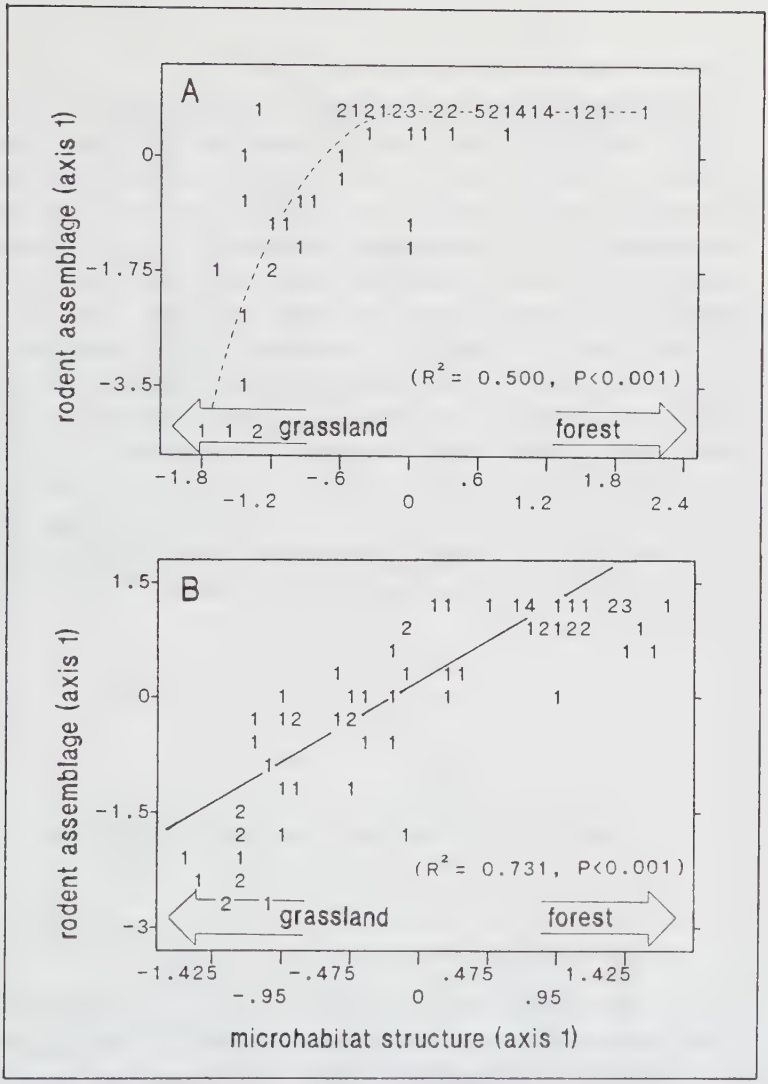


Fig. 37. Relationships between first CCA axis derived from species and environmental variables scores for winter (n=63) (A) and pooled captures (n=69) (B). Multiple coefficients of determination (R^2) derived by regression show the amount of variation in rodent captures explained by the microhabitat attributes (dotted curve eye-adjusted).

and the pooled analysis (73.09%). The asymptotic response curve for the winter data suggests a high habitat discrimination by rodents and a threshold level of habitat structure, above which the species do not so readly discriminate. This fact might be related to the landscape features. The main vegetation zones such as grasslands and forests are more discriminated. Within these, the microhabitats are less discriminated by the species. The more linear and stronger relations observed for the pooled data (Fig. 37.b) suggest that the changes in the assemblages composition, between the sampling sites, may occur at a more similar rate, with less discontinuity between them. Although seasonal differences appear to differentiate the rodent composition, in a yearly pattern the species tend to use more homogeneously the available habitats.

2.1.5. HABITAT STRUCTURE AND SPECIES INTERACTIONS

The distribution of captures during the summer and winter resulted in a low number of unfilled trap sites in each season. It suggests that the captures were not independent and that some "trap competition" might occur. When compared with the ' Poisson distribution, the distribution of captures suggested some interdependence (G_{adj}=56.88; G_{adj}=32.57; d.f.=7, $P<0.01$; summer and winter respectively) (Fig. 38). They were not random between the trap sites. The decrease in the frequencies of sites with

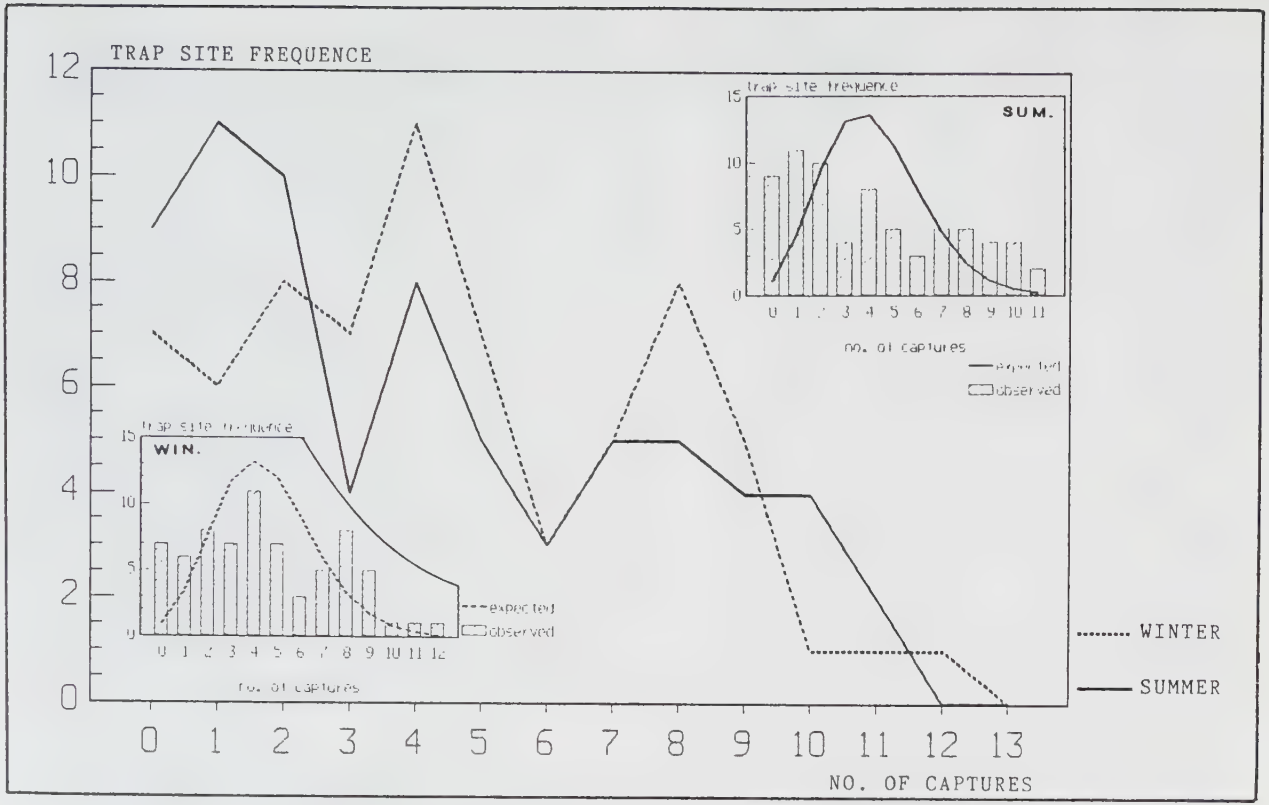


Fig. 38. Comparison of the observed frequency distribution of rodent captures among the trap sites with the expected frequencies of captures based on the Poisson distribution. sum. = summer, win. = winter.

low number of captures in winter and the increase of those with higher number were not significant (G_{adj}=8.91, d.f.=9, P>0.25). Only small changes in habitat use by the whole community were observed, allowing some analysis pooling the data.

A large body of evidence indicates that many coexisting species of small mammals interact competitively (BROWN, 1978; BROWN and BOWERS, 1984; BROWN et al, 1986; GRANT, 1972, 1978; MESERVE, 1981; SCHOENER, 1974a; FRAMSTAD and STENSETH, 1984), and the habitat segregation between species is frequently attributed to competition (DUESER and PORTER, 1986; GRANT, 1972; HALLETT, 1982; SCHOENER, 1974a, 1974b). On the other hand, the actual pattern on habitat use among species may have evolved as a result of past competition (ROSENZWEIG, 1974, 1977; PIMM and ROSENZWEIG, 1981) or by specific habitat requirements (FRAMSTAD and STENSETH, 1984) making the interaction very weak or not detectable at present. The comparison of co-occurrences between species in trap sites, could provide some evidences about the community structure and the species-microhabitat relations. Certainly some habitats may be more intensively selected than others originating associated distribution among the rodents. In other cases the co-occurrence may be only by chance, as a result of individual dispersal between the vegetation zones. The negative association which increases the probability of no joint occurrence, could be explained by differences in habitat use, and by some other factors that may partially be related to the microhabitat structure.

No positive association among the captures was observed between any two species at any time. However, a negative and significant correlation (P<0.05) was observed for almost all the pairs of species, at least in one season (Tab. 14), except to *S.tumidus* and *D. kempi*, *A serrensis* and *O. delticola*, and *O. rufus* and *D. kempi*.

	OXYRUF	DELKEM	AKOAZA	AKOSER	SCATUM	ORYFLA	ORYDEL
OXYRUF		-0.457	-0.577*	-0.234	-0.700**	-0.374	-0.533**
DELKEM	-0.421		-0.520*	-0.132	-0.261	-0.524*	-0.511**
AKOAZA	-0.847*	-0.605*		-0.288*	-0.506*	-0.543*	-0.639***
AKOSER	-0.354*	-0.411**	-0.339*		-0.138	-0.328*	-0.200
SCATUM	-0.397	-0.190	-0.355	-0.382**		-0.661**	-0.572***
ORYFLA	-0.547*	-0.508**	-0.440	-0.566***	-0.447*		-0.450*
ORYDEL	-0.944***	-0.676**	-0.791	-0.097	-0.421	-0.423	

Table 14. Simple correlation coefficients based on the numbers of rodent captures. The lower left triangle contains the winter correlations; the upper right triangle, summer correlations. * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

S. tumidus and *D. kempi* presented no significant association in summer and in winter ($P>0.10$). In both seasons the great number of captures of *D. kempi* was in the wet grassland (55.6% in summer and 33.3% in winter). *S. tumidus* was more frequent in the swamp forest (33.3%, 36.8%, summer and winter respectively) (Tab. 7 and Tab. 8). Both species used transitional habitats with relative frequency but positive or negative relations were not evident. The captures of *O. delticola* and *A. serrensis* in the two seasons were not significantly correlated ($P>0.10$) despite the great affinity of both species to the swamp forest. In the first season *O. delticola* was scarce. In the second the great number of captures was in the swamp forest as also observed for *A. serrensis*.

The stepwise regression to estimate the unique effect of the habitat variables and of the species variables together on each species, showed that the full set explains partially the variations observed. For the winter data (Tab. 15) the set of environmental and species variables explain significantly ($P<0.05$) the distribution of captures of *D. kempi* and *A. serrensis*. *O. delticola* was less affected by this variables set ($0.10>P>0.05$) and no significant correlation was observed for the other species. The lack of significance ($P>0.30$) in the change of the multiple semipartial correlation coefficients for the species variables (R_s^2), after entering the environmental variables in the first step, showed that no species was significantly affected by the remaining components of the community. However, *O. flavescens* and *O. rufus*, two species with small niche breadth, presented greater species interaction coefficients (R_s^2). It seems likely that the restriction in the habitat use by both species may be resulted of weak interaction with the remaining part of the assemblage. *O. flavescens* showed the lowest (11.55%) and *A. serrensis* the highest (81.53%) proportion of variation attributed to both habitat and species variables. The preponderance of high positive ratio in the proportion of the total variation attributed to species and habitat variables suggest that the habitat has a great unique effect, since the interactions between all species were apparently weak.

The analysis by pooling the captures of both seasons, revealed similar trends, but only to *O. rufus* and *O. flavescens* the addition of habitat variables to a model already containing species variables produced no significant changes in R_h^2 ($P>0.50$) (Tab. 16). This suggests that both species are relatively independent of the environmental variables, at least in the habitat utilized. No species appears to be affected by the remaining components of the community ($P>0.10$), and the

SPECIES	Overall R_{hs}^2	Habitat R_h^2	Species R_s^2	Difference $R_h^2 - R_s^2$	Percent(%) $R_h^2 - R_s^2 / R_{hs}^2$
O. rufus	0.471	0.366	0.102	0.264	56.05
D. kempi	0.551**	0.453**	0.042	0.411	74.59
A. azarae	0.452	0.318	0.085	0.233	51.55
A. serrensis	0.704***	0.597***	0.023	0.574	81.53
S. tumidus	0.381	0.333	0.043	0.290	76.12
O. flavescens	0.277	0.157	0.125	0.032	11.55
O. delticola	0.488*	0.381*	0.047	0.334	68.44

* P<0.10 ** P<0.05 *** P<0.001

Table 15. Squared multiple semipartial correlation coefficients (R) for sets of habitat (h) and species(s) variables for the winter data. The overall R_{hs}^2 is the coefficient of determination when both sets of variables (habitat and species) are included in the analysis. The habitat R_h^2 is the change in the overall R^2 resulting from the addition of habitat variables to a regression model containing the species variables. The species R^2 is the quantity attributable to adding the block of species variables to a model containing habitat variables. The proportion of total variation attributable to habitat and species variables are provided in the last column. The more positive the total variance (%) attributable to habitat and species variables the greater the abundances are influenced by the habitat variables.

SPECIES	Overall R_{hs}^2	Habitat R_h^2	Species R_s^2	Difference $R_h^2 - R_s^2$	Percent(%) $R_h^2 - R_s^2 / R_{hs}^2$
O. rufus	0.208	0.164	0.032	0.132	63.46
D. kempi	0.591***	0.412***	0.037	0.375	63.45
A. azarae	0.387+	0.319*	0.059	0.274	70.80
A. serrensis	0.598***	0.413***	0.045	0.368	61.54
S. tumidus	0.526**	0.340**	0.048	0.292	55.51
O. flavescens	0.294	0.176	0.077	0.099	33.67
O. delticola	0.556***	0.436***	0.098	0.338	60.79

+ P<0.10 * P<0.05 ** P<0.01 *** P<0.001

Table 16. Squared multiple semipartial correlation coefficients (R^2) for sets of habitat (h) and species(s) variables for the pooled data (summer and winter). For further information see Tab. 15.

habitat variables accounted for a substantial proportions of the observed variation. *O. flavescens* showed the lowest proportion of total variation attributed to species and habitat variables.

The multiple regression analysis for each species (as dependent variable) forcing other species (as independent variables) to enter the regression separately, but after the habitat variables were added to the model, showed that normally pairwise effects of interactions on the assemblage are not important (Tab. 17). Only one pair of species - *A. serrensis* and *O. delticola* - with the pooled captures of the two seasons, showed a significant increase of the multiple partial correlation coefficient (P<0.05) by interaction effect. Both species are more related to forest sites and interactions on microhabitat use may be favoured. Such coefficient (R^2 change) was symmetrical

Table 17. Community matrix of interaction coefficients for species pairs. R_h^2 = coeficient of determination for the regression equations based on the environmental variables set. R_{hs}^2 = overall coefficient that includes habitat and species variables. $R_{hs}^2 - R_h^2$ = the quantity attributable to the species when added to the model that already contains the set of habitat variables.

Species	Habitat R_h^2	Species added	Overall R_{hs}^2	Change $R_{hs}^2 - R_h^2$
O. rufus	0.177	*D. kempi*	0.177	0.000
		A. azarae	0.177	0.000
		A. serrensis	0.177	0.000
		S. tumidus	0.186	0.009
		O. flavescens	0.177	0.000
		O. delticola	0.191	0.014
D. kempi	0.554***	*O. rufus*	0.555	0.001
		A. azarae	0.572	0.018
		A. serrensis	0.555	0.001
		S. tumidus	0.558	0.004
		O. flavescens	0.567	0.013
		O. delticola	0.555	0.001
A. azarae	0.328*	*O. rufus*	0.329	0.001
		D. kempi	0.355	0.027
		A. serrensis	0.330	0.002
		S. tumidus	0.338	0.010
		O. flavescens	0.335	0.007
		O. delticola	0.339	0.011

* P<0.05 *** P<0.001

(to be continued)

Species	Habitat R_h^2	Species added	Overall R_{hs}^2	Change $R_{hs}^2 - R_h^2$
A. serrensis	0.552***	*O. rufus*	0.553	0.001
		D. kempi	0.554	0.002
		A. azarae	0.553	0.001
		S. tumidus	0.562	0.010
		O. flavescens	0.553	0.001
		O. delticola	0.587	0.035*
S. tumidus	0.477***	*O. rufus*	0.483	0.006
		D. kempi	0.482	0.005
		A. azarae	0.485	0.008
		A. serrensis	0.488	0.011
		O. flavescens	0.481	0.004
		O. delticola	0.496	0.019
O. flavescens	0.217	*O. rufus*	0.218	0.001
		D. kempi	0.239	0.022
		A. azarae	0.225	0.008
		A. serrensis	0.219	0.002
		S. tumidus	0.223	0.006
		O. delticola	0.249	0.032
O. delticola	0.458***	*O. rufus*	0.467	0.009
		D. kempi	0.459	0.001
		A. azarae	0.466	0.008
		A. serrensis	0.499	0.041*
		S. tumidus	0.477	0.019
		O. flavescens	0.480	0.022

* P<0.05; *** P<0.001

suggesting no dominance among the two species. To the other species, the differences in habitat use certainly prevent significant direct interactions. Only to *O. rufus* and *O. flavescens* the multiple coefficient of determination with the full set of habitat variables was not significant ($P>0.30$). This indicates that the habitat structure does not affect their occurrence, at least in the habitats utilized.

No species has significant interaction with *O. rufus* and *O. flavescens* ($P>0.10$). They certainly use the microhabitats in a manner not determined by any other component of the community. *O. rufus* inhabits a restricted variety of habitats that reduce the probabilitiy of interaction with the other species. *O. flavescens*, more largely distributed, appears to be an opportunist with no defined relations, at least regarding the habitat variables set and the species separately.

The virtual absence of significant interactions between the species in the assemblage may be reinforced by the tendency for habitat selection, that results in a particular sort of species among the habitats. Some species were associated primarily with herbaceous vegetation and some with woody. Except for one pair of species, all the partial regression coefficients were not significant, indicating that mutual inhibitory relationships between species are not common in the assemblage.

2.2. CAPÃO DO LEÃO

2.2.1. OVERALL HABITAT STRUCTURAL SIMILARITIES

The overall structural similarity between the habitats sampled in the Capão do Leão region considering the mean values of the seventeen structural variables (Tab. 18) showed two groups of similarity (Fig. 39) (r_{cd}=0.683, P<0.05). The first group is composed by the swamp forest interior, swamp forest edge, and the sand forest. The second one is formed by the grassland and the corridors. The forest types are contiguous and sharply separated by a high inactive cliff that delimits the sandy and the lagoonal terraces (Fig. 6), whereas the grasslands and corridors are limited to the lower area.

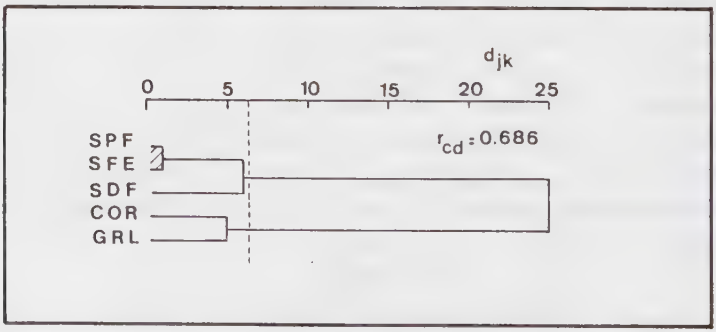


Fig. 39. Dendrogram of habitat structural relationships. d_{jk} = structural distance (Euclidean distance - rescaled). The dashed line represents the mean Euclidean distance (d_{jk}). The diagonal shading area demarcates the group with high structural similarity ($\bar{d}_{jk}$-s). r_{cd}= cophenetic correlation.

Habitat Variable	SPF	SDF	SFE	COR	GRL
HHT	51.34	48.45	41.16	52.83	34.18
HCV	57.94	77.84	77.03	81.86	97.73
FHD25	6.26	6.36	10.30	15.55	22.38
FHD50	16.40	14.91	21.79	30.72	41.29
FHD100	33.68	30.45	41.28	51.88	65.71
FHD170	39.01	42.23	56.54	60.75	75.70
CANHT	7.96	7.69	6.24	2.39	0.00
CANCV	74.57	13.97	42.57	5.94	1.35
TDIA	28.24	38.71	23.28	14.84	0.00
TDIS	1.27	0.23	0.80	0.19	0.06
BRANCH	1.76	0.87	1.59	0.23	0.00
FLOG	22.64	7.86	13.36	4.17	0.00
SHRUB	15.91	2.29	19.00	6.67	0.67
ROHIHO	5.55	2.00	2.70	0.67	0.00
LIT	3.43	3.52	2.12	1.19	0.20
MUD	2.26	0.00	10.88	10.34	0.02
FLOOD	8.63	0.00	18.71	38.17	22.22

Table 18. Sample estimates of the mean for the seventeen habitat variables for each habitat type. The acronyms are from Tab. 1. SPF = swamp forest; SDF = sand forest; SFE = swamp forest edge; COR = corridors; GRL = grassland.

2.2.2. HABITAT GRADIENTS

The cluster analysis of the distance matrix (Tab. 19) of the mean CCA scores based on the linear combination of the environmental variables showed three main groups of habitats ($d_{jk}<d_{jk}$-s) (r_{cd}=0.673, 0.05>P>0.01) differently related to the first and the second canonical axis (Fig. 40): swamp forest interior, swamp forest edge together with the sand forest, and the habitats where the forest features are less expressive - grassland and corridors. Nevertheless, by the criterion $d_{jk}<\overline{d_{jk}}$, the forest habitats are more similar. The canonical coefficients and the correlations of the environmental variables (tab. 20) in the CCA showed that the first axis is a forest - grassland gradient. The swamp forest sites have high herb layer but normally dry soils. This may in part be related to the artificial drain canals that attenuate the swampy features of the region. The grassland sites and the corridors along fences, at the other extreme of the gradient, have normally low herbaceous height but high foliage density and wet or muddy soils. The second axis presented a gradient of variation inside the contiguous forests. Although the sand forest with dry sites and low herb layer shows a continuity to the swamp forest, it is located on the high sandy pleistocene terrace (CECO, 1988) at least 7 meters above the lower lagoonal plain. The swamp forest edge is less related to the axis and therefore, to the environmental variables set. The fallen logs and the aggregation of trees determine the main features of this area, which presents transitional features between the sites inside the swamp forest and the other habitat types. The forest edge was partially

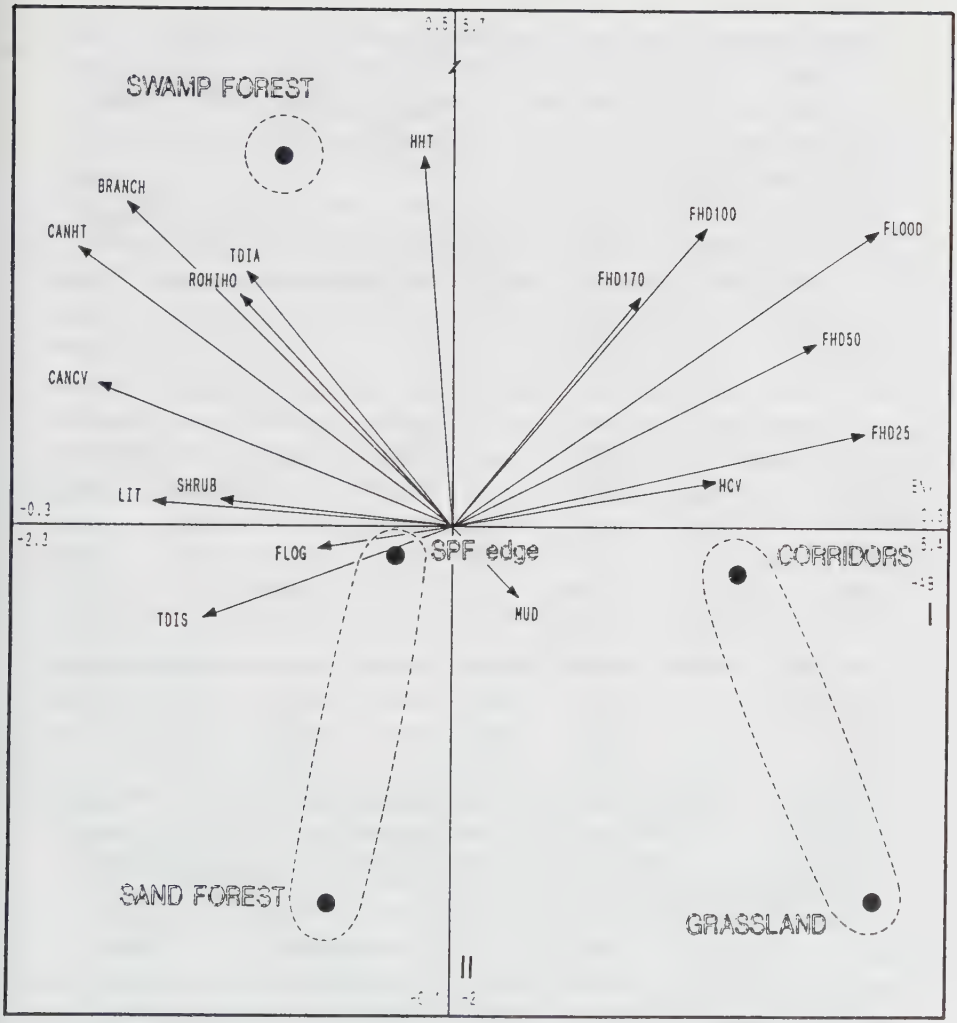


Fig. 40. Canonical Correspondence Analysis (CCA) diagram with habitat centroids (mean scores of the CCA which are linear combination of environmental variables) on the first two axis for the Capão do Leão region (41 trap sites). The dotted lines delimit the three groups whose Euclidean distance between the centroids is less than $\bar{d}_{jk}$ - s of the distance matrix. SPF = swamp forest. The environmental variable acronyms are from Tab. 1.

delimited by logging, and consequently resulting in an increase in the grassland area in detriment of the swamp forest. The dry grassland on the high terrace and adjacent to the sample habitats (not included in the diagram), presented low herb layer (usually less than 10 cm high) due to intensive livestock grazing. The habitat structure appears unfavorable to the species trapped in the region. Only skulls and mandibles of *O. flavescens* were found near burrowing owl (*Athene cunicularia*) burrows.

	SPF	SDF	SFE	COR	GRL
SPF	0.00				
SDF	2.43	0.00			
SFE	1.37	1.14	0.00		
COR	2.21	1.88	1.33	0.00	
GRL	3.29	2.03	2.12	1.17	0.00

$\bar{d}_{jk}$=1.895

s=0.674

Table 19. Euclidean Distance (d_{jk}) between the habitat centroids related to first and second axis. SPF = swamp forest; SDF = sand forest; SFE = swamp forest edge; COR = corridors; GRL = grassland.

	Canonical coefficients				Correlation coefficients			
AXIS	1	2	3	4	1	2	3	4
variable								
HHT	-0.04	0.05	-0.02	0.01	-0.05	0.23	-0.13	-0.02
HCV	-0.01	-0.03	0.09	-0.03	0.39	0.02	0.07	-0.01
FHD25*	0.25	0.11	-0.02	-0.03	0.59	0.05	0.04	0.09
FHD50*	-0.31	-0.17	0.05	0.02	0.53	0.11	0.03	0.15
FHD100*	0.30	0.05	0.00	0.10	0.37	0.19	0.00	0.17
FHD170*	-0.25	0.05	-0.02	-0.08	0.27	0.15	-0.01	0.13
CANHT	-0.05	0.05	-0.04	0.01	-0.55	0.18	-0.09	-0.06
CANCV	-0.09	0.06	0.10	-0.03	-0.51	0.09	0.10	-0.04
TDIA	-0.05	-0.02	-0.02	-0.01	-0.29	0.16	-0.13	-0.07
TDIS	-0.01	-0.06	-0.01	0.02	-0.36	-0.08	-0.03	-0.03
BRANCH	0.04	0.00	0.01	0.01	-0.47	0.20	0.83	-0.05
FLOG	-0.01	-0.02	0.00	-0.02	-0.19	-0.02	0.01	-0.19
SHRUB	-0.03	0.01	-0.04	0.03	-0.33	0.01	-0.06	-0.10
ROHIHO	0.05	0.03	0.03	-0.04	-0.31	0.14	0.16	-0.20
LIT	-0.03	-0.01	0.01	-0.04	-0.42	0.00	0.09	-0.12
MUD	-0.01	-0.04	0.00	-0.04	0.10	-0.06	-0.25	-0.12
FLOOD*	0.11	0.05	-0.03	-0.04	0.62	0.18	-0.21	-0.06

Table 20. Canonical coefficients and intra-set correlations of environmental variables with the first four axis of Canonical Correspondence Analysis (CCA) for Capão do Leão data. The environmental variables were standardized to unit variance after log-transformation. Variable acronyms are from Tab. 1. * = variables with t-value <0.05.

2.2.3. RODENTS HABITAT USE

The total captures of rodents (CItot) in the surveyed habitats increased from the grassland to the forest and corridors (Tab. 21). The highest index of captures was obtained at the swamp forest edge and *O. delticola* was always the numerically dominant species, except in the grassland, where only *O. flavescens* was captured. The community as a whole does not use the habitat types proportionally to their representation according to the sampling effort (G_{adj}=12.61, d.f=4, P<0.05). The captures in the swamp forest edge - the transitional habitat to the grassland - were much higher than expected (Fig. 41.a). The sand forest appears to be used in the proportion near its relative availability. The grassland appears to be relatively unsuitable habitat. In the forest, ecotones, and grassland, the pooled captures were not distributed in proportion expected by the relative sampling effort (G_{adj}=9.22, d.f.=2, P<0.01), but the numerical dominance of *O. delticola* limits the interpretation of the data. The transitional habitats were favoured, in opposition to the grassland. In the forests, the pooled captures were as virtually expected.

O. delticola was normally more associated with forests and transitional microhabitats (Fig. 41.b). The observed captures differed significantly from expected (G_{adj}=18.77, d.f.=4, P<0.001) and were more abundant in the swamp forest edges and in the sand forest. The swamp forest appears to be used in a proportion near its relative availability. The low number of captures in the corridors suggested that these are used with some restriction. The grassland was largely avoided. *O. flavescens* was trapped

only in the grassland and in the corridors along fences margined by the grassland. The grassland microhabitats seem to represent their core area as in other regions (this work; BARLOW, 1969; OLIVEIRA, 1991). *O. ratticeps* was trapped at the edge and inside the swamp forest which seems to be its main area in that region. *S. tumidus* was trapped only in the corridors. The livestock grazing certainly limits its occurrence in the grasslands. The species is probably absent in extensive areas on the high sandy terrace since its typical microhabitat is normally lacking. *H. brasiliensis*, a species normally associated to grassy marsh areas and highly covered dry grassland, was trapped at the swamp forest edges and in the corridors along fences. The forest edge is not its typical microhabitat and certainly it is used only as refuge.

	SPF	SDF	SFE	COR	GRL	Totals
S. tumidus				3		3
				(0.64)		
O. flavescens				3	3	6
				(0.64)	(0.83)	
O. delticola	14	7	20	5		46
	(2.05)	(3.24)	(4.13)	(1.07)		
O. ratticeps	3		2			5
	(0.44)		(0.41)			
H. brasiliensis			1	1		2
			(0.21)	(0.21)		
NSC	2	1	3	4	1	
Totals	17	7	23	12	3	62
CItot	(2.49)	(3.24)	(4.75)	(2.56)	(0.83)	
Trap-days	684	216	484	468	360	2212

Table 21. Capão do Leão region. Number of captures of each species by habitat category. In parentheses, the capture index CI (%) based on trapdays *per* habitat. SPF = swamp forest; SDF = sand forest; SFE = swamp forest edge; COR = corridors; GRL = grassland; NSC = number of species caught.

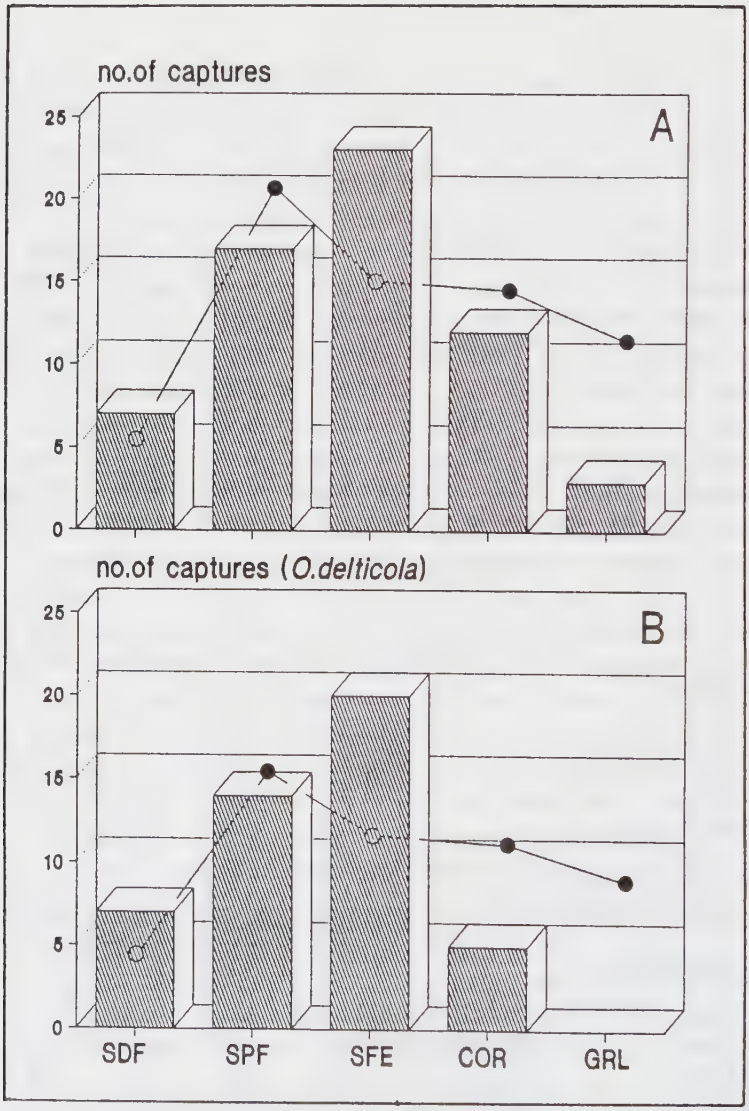


Fig. 41. Observed and expected number of all rodent captures (A) and *O. delticola* (B) in five habitats in Capão do Leão region (cf. Tab. 41). SDF= sand forest; SPF= swamp forest; SFE= swamp forest edge; COR= corridors; GRL= grassland.

2.2.4. SPECIES / HABITAT STRUCTURE RELATIONSHIPS

In a bivariate correlation analysis with the total rodent captures (CI_{tot}) and the mean values of the structural variables *per* habitat a significant correlation was observed with CANHT, canopy height ($r=0.878$, $P=0.05$), and TDIA, mean tree trunk diameter ($r=0.910$, $P<0.05$). In a multiple regression analysis by the stepwise procedure only the variable TDIA was selected as predictor ($P<0.05$). All these variables, however, are not directly related to the rodent species but showed that the grassy habitats, or those partially logged, present some use restriction by the assemblage. Such pattern may result in part from livestock grazing disturbance, since the assemblage is composed of some species commonly associated to grasslands. The number of rodent species caught (NSC) was correlated only with the relative importance of mud (MUD) ($r=0.957$; $P<0.05$), the single variable selected in a multiple regression stepwise procedure ($P=0.01$). This variable has no defined relation to the species but shows that the sites on the lagunar terrace tend to sustain a more diverse rodent assemblage.

Among the seventeen variables measured at each positive trap site five of them (Tab. 20) fitted very well the species data (t-tests; $P<0.05$). They contribute significantly to the multiple regression in the canonical ordination and constitute a subset of environmental variables that explain equally well as the full set, the species-environment biplot. The variable FLOOD present on the low lagoonal terrace ($t=3.72$; $d.f.=23$, $P<0.01$) composed together with the foliage height density variables set (FHD25, $t=2.79$; FHD50, $t=2.37$; FHD100, $t=2.60$; $P<0.05$;

FHD170, t=3.01, P<0.01) the main group of variables that has a large effect on rodent distribution. The foliage height densities are certainly the critical factors since they constitute the main structure of the grassland and vary largely in forest sites. They are negatively correlated (APPENDIX. 3) with canopy cover (CANCV, P<0.001), tree dispersion (TDIS, P<0.01), fallen logs (FLOG, P<0.05), and potential rodents' hiding holes (ROHIHO, P<0.01) which characterize the forest sites.

The first and the second axis of the CCA accounted for 74.3% of the main variation observed in the species-environment biplot of CCA (Tab. 22). The first eigenvalue (λ_1=0.77) was significant (MCptλ_1, P=0.01) showing an appreciable relation between the rodent species and the environmental variables. The first CCA axis (λ_1=0.77) (Fig. 42) seems to separate the species more related to grassland and forest habitats as well as those related to wet and dry sites. The second axis (λ_2=0.25) separates the species along a herbaceous height gradient from those more related to sites with high foliage height density.

	AXIS			
	1	2	3	4
Eigenvalue	0.77	0.25	0.21	0.14
% Var. acc. for	56.26	18.02	15.42	10.30
Cum. % var. acc.	56.26	74.28	89.70	100.00

Table 22. Capão do Leão region. Eigenvalue, percentage of total variance, and cumulative percentage attributable to each axis in the Canonical Correspondence Analysis (CCA).

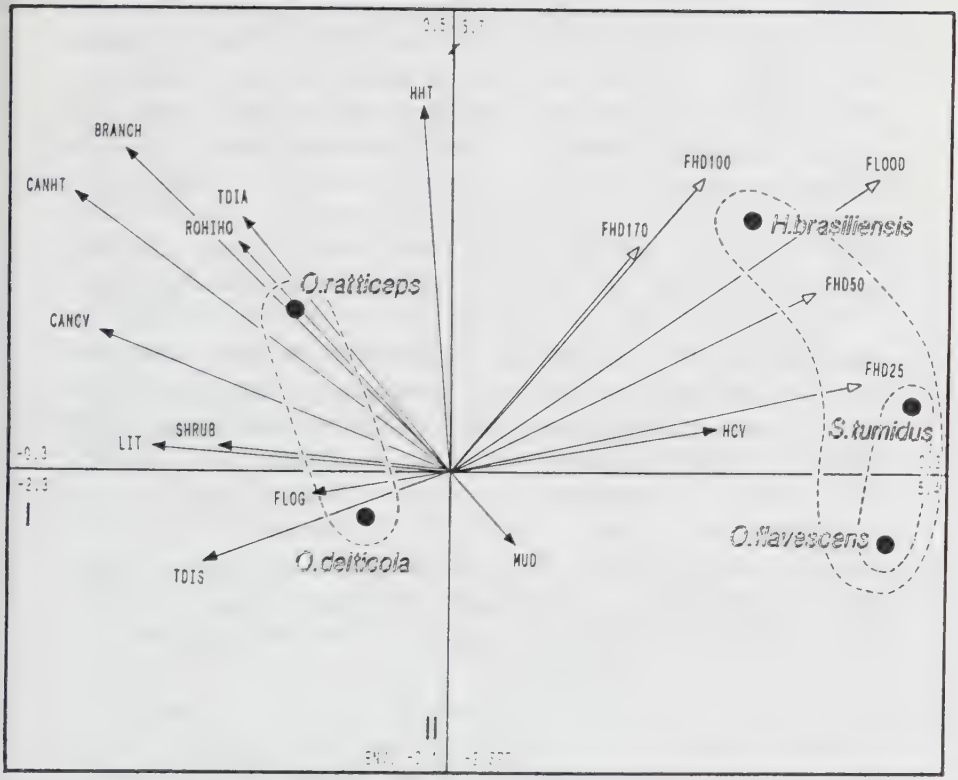


Fig. 42. Ordination diagram based on Canonical Correspondence Analysis (CCA) of rodent species data with respect to microhabitat structure (for total species caught see Tab. 21). The dotted lines delimit the two groups whose Euclidean distance between the centroids is less than the mean Euclidean distance ($d_{\overline{jk}}$) between the CCA scores. The open arrows are the variables that explains the species data almost equally well as the full set (t-value <0.05). The environmental variable acronyms are from Tab. 1.

The degree of similarity between the species (d_{ij}) in relation to the canonical axis showed two groups (Fig. 42) that result from the cluster analysis of the distance matrix (Tab. 24) of the CCA species scores (Tab. 23). These groups are clearly related to the two major habitats - forest and grassland - and represent some internal heterogeneities related to the main features of each unit. The *S. tumidus*, *O. flavescens* and *H. brasiliensis* centroids lie on the right-hand side of the diagram showing a high relation with the herbaceous layer features. The first two species are related to sites with high ground cover (HCV) and high foliage height density near the ground (FHD25). *O. flavescens* is less related to wet sites and presented highly negative correlation with variables that characterize forest microhabitats - CANCV, FLOG, LIT - in contrast to *H. brasiliensis*, that is more related to wet sites with high foliage height density, the transitional microhabitats. The other group - *O. delticola* and *O. ratticeps* - is negatively correlated with all variables that describe herbaceous layer features and is

	AXIS			
	1	2	3	4
S. tumidus	4.37	0.70	-1.06	-2.48
O. flavescens	4.12	-0.67	1.10	0.52
O. delticola	-0.87	-0.31	-0.21	0.01
O. ratticeps	-1.58	1.71	1.46	-0.29
H. brasiliensis	2.78	2.40	-1.95	1.81

Table 23. Species scores on four Canonical Correspondence Analysis (CCA) ordination axis for the Capão do Leão data.

	SCATUM	ORYFLA	ORYDEL	ORYRAT	HOLBRA
SCATUM	0.00				
ORYFLA	1.06	0.00			
ORYDEL	2.02	1.80	0.00		
ORYRAT	2.26	2.73	1.57	0.00	
HOLBRA	1.42	2.41	2.45	1.64	0.00

$\overline{d_{jk}}$=1.936

s=0.528

Table 24. Euclidean Distance (d_{jk}) between the species centroids related to first and second axis. SCATUM = *S. tumidus*; ORYFLA = *O. flavescens*; ORYDEL = *O. delticola*; ORYRAT = *O. ratticeps*; HOLBRA = *H. brasiliensis*.

more related to those that characterize forest sites. The *O. ratticeps* centroid lies on the upper left-hand side of the diagram, near the main environmental variables that describe the forest microhabitat features. The availability of shelters (ROHIHO) may be a critical factor that affects the occurrence of this large *Oryzomys* species. The captures of *O. ratticeps* in the north of the Coastal Plain (pers. observ.) were normally associated with sites presenting complex ground features. In those regions the species was observed climbing almost branchless trees (up to 7 m high) with approximately 10 cm diameter. This could be an evidence that the species is not strictly terrestrial as reported earlier (ALHO, 1982).

O. delticola, the more centered species in the diagram, has the lowest weighted average with the first two axis (Tab. 23) and, consequently, with the environmental variables set that characterizes them. The species is related to forest sites with low ground cover, and low

foliage height density. The correlations with the trees spatial disposition (TDIS), suggest scansorial habit that normally is assigned to this species (LANGGUTH, 1963; BARLOW, 1969; OLIVEIRA, 1985).

The first partial CCA eigenvalue subjected to the Monte Carlo permutation test with the variables set related to forest sites (CANCV, CANHT, TDIS, TDIA, BRANCH, and FLOG) fitted as covariables was not significant ($MCpt\lambda_1$=0.33). This fact suggests that much of the observed variations in the species captures may be related to a set common to all other habitat types as ground layer features. The partial CCA fitting the herb layer variables set (HHT, HCV, FHD25, FHD50, FHD100, and FHD170) as covariables was not significant ($MCpt\lambda_1$, P=0.37) showing that the rodent distribution is affected by them. The CCA performed only with the herb layer variables set showed that its effect was near the margin of significance ($MCpt\lambda_1$, P=0.08). This suggests that among these variables, some subsets may affect the rodents, more than other sets. Among the several subsets tested, only the foliage height density variables ($MCpt\lambda_1$, P=0.03), and the herbaceous height and cover, associated with flooded areas, explain significantly the observed variance ($MCpt\lambda_1$, P=0.01). The herbaceous layer features vary between the sites but compose the main ground habitat structure in several areas. The maximal expressiveness is found in the transitional microhabitats, grasslands and corridors. The lowest ground cover values were observed in the swamp forest. However, higher values were also found in this area. The corridors are largely structured near the ground surface and certainly the trees have low effect on the rodent distribution.

The performed analysis considered the rodents relationships only within the habitat types, but not in the landscape as a whole. The rodent distribution is

determined partially by the main features of the landscape - high sandy terrace and low lagoonal plain - since they determine the vegetation zones. The low areas on the lagoonal terrace have a rich rodent assemblage as compared to those of the high sandy terrace where the semiaquatic species (*H. brasiliensis* and *S. tumidus*), judging by the microhabitat distribution, may be absent in extensive areas. However, the livestock grazing effects on habitat structure are greater in this area than in the lower lagoonal terrace and certainly prevent the high occurrence of any rodent species. It seems more likely that in the pristine habitats the differences between the rodent community responses would be less underlined.

2.3. FAXINAL

2.3.1. OVERALL HABITAT STRUCTURAL SIMILARITIES

The overall structural similarity between the habitats in the Faxinal region calculated by the stratified samples showed three main habitat groups ($d_{jk}<\overline{d_{jk}}$) resulting from the cluster analysis of the Euclidean distance based on the mean values of the environmental variables (Tab. 25): the forest habitat types, the shrubland/thicket group, and the Butiá savanna (Fig. 43) (Tab. 26). A high cophenetic correlation was observed (r_{cd}=0.831, P<0.01). The forest habitat types (swamp forest and mesic swamp forest) on the lower lagoonal terrace (CECO, 1984) compose an unity. The second major group comprises two subgroups: shrubland/thicket and Butiá savanna. The first subgroup presents high structural similarity ($d_{jk}<\overline{d_{jk}}$-s) and is composed of the open canopy shrubland (hereafter referred to as shrubland) and the thicket (closed canopy shrubland) habitats; the second subgroup is composed only of the Butiá savanna on the high sandy terrace. Nevertheless, such area is less related to the shrubland-forest relative chronosequence despite the structural similarity to areas of secondary growth.

Habitat Variable	SPF	MSF	TKT	SBL	BTS
HHT	54.43	34.61	37.03	74.36	76.95
HCV	42.00	31.30	37.75	80.50	68.50
FHD25	6.75	8.57	13.12	10.29	7.14
FHD50	17.65	16.88	24.11	24.80	17.18
FHD100	32.18	30.09	37.82	57.78	38.91
FHD170	39.21	41.75	45.21	74.65	60.93
CANHT	9.09	10.60	4.44	2.80	1.97
CANCV	69.30	82.70	68.40	13.80	1.90
TDIA	22.27	18.89	11.63	15.98	26.30
TDIS	1.51	1.40	0.10	0.06	2.03
BRANCH	3.17	3.46	0.00	0.28	0.00
FLOG	37.73	14.76	5.50	26.65	18.50
SHRUB	19.47	24.86	61.13	5.67	0.00
ROHIHO	10.23	9.61	4.38	1.25	0.00
LIT	4.37	7.22	11.54	7.91	1.27
MUD	16.85	18.27	10.75	0.30	0.00
FLOOD	47.40	1.60	0.00	0.90	0.00

Table 25. Sample estimates of the mean for seventeen habitat variables for each habitat type. Variable acronyms are from Tab. 1. SPF= swamp forest; MSF= mesic swamp forest; TKT = thicket; SBL = shrubland; BTS = Butiá savanna.

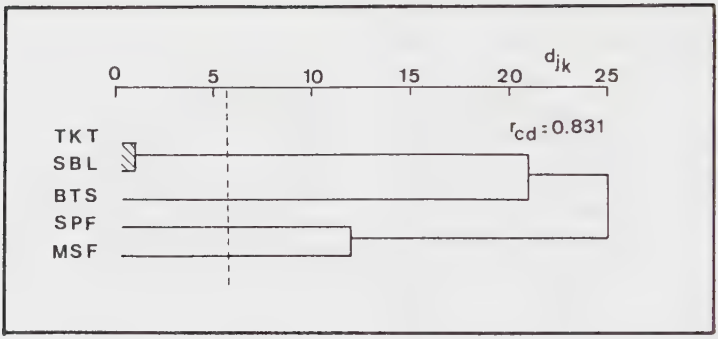


Fig. 43. Dendrogram of habitat structural relationships. d_{jk} = structural distance (Euclidean distance). The dashed line represents the mean Euclidean distance ($\overline{d_{jk}}$). The diagonal shading area demarcates the group with high structural similarity ($\overline{d_{jk}}$-s). TKT = thicket; SBL = shrubland; BTS = Butiá savanna; SPF = swamp forest; MSF = mesic swamp forest. r_{cd} = cophenetic correlation.

	SPF	MSF	TKT	SBL	BTS
SPF	0.00				
MSF	3.37	0.00			
TKT	6.42	4.82	0.00		
SBL	6.61	6.61	5.27	0.00	
BTS	5.49	5.77	6.67	4.59	0.00

$\overline{d_{jk}}$ = 5.56

s = 1.08

Table 26 Euclidean Distance (d_{jk}) between the habitats based on mean values of the environmental variables. SPF= swamp forest; MSF= mesic swamp forest; TKT = thicket; SBL = shrubland; BTS = Butiá savanna.

2.3.2. HABITAT GRADIENTS

The canonical ordination excluding the Butiá savanna showed that the first axis is not a simple chronosequence as expected by the general features of the region. The gradients are not clear because some habitat types such as shrublands and thickets (seral stages of secondary succession) are largely separated. Both habitats are not grouped in the same cluster (Fig. 44), mainly due to the canopy cover that affects the herb layer features and separates largely the two habitat types. The Table 27 presents the Euclidean distance between the mean habitat scores of CCA used to delimit the similar groups.

	SPF	MSF	TKT	SBL
SPF	0.00	1.26	2.46	0.71
MSF	1.62	0.00	1.55	1.97
TKT	2.84	1.35	0.00	3.09
SBL	1.59	1.87	2.35	0.00
$\overline{d_{jk12}}$ = 1.840			$\overline{d_{jk23}}$ = 1.937	
s = 0.855			s = 0.558	

Table 27. Euclidean distance (d_{jk}) between the habitat centroids. Above the diagonal d_{jk} on the first and the second axis; under the diagonal d_{jk} on the second and third axis. SPF= swamp forest; MSF= mesic swamp forest; TKT = thicket; SBL = shrubland; BTS = Butiá savanna.

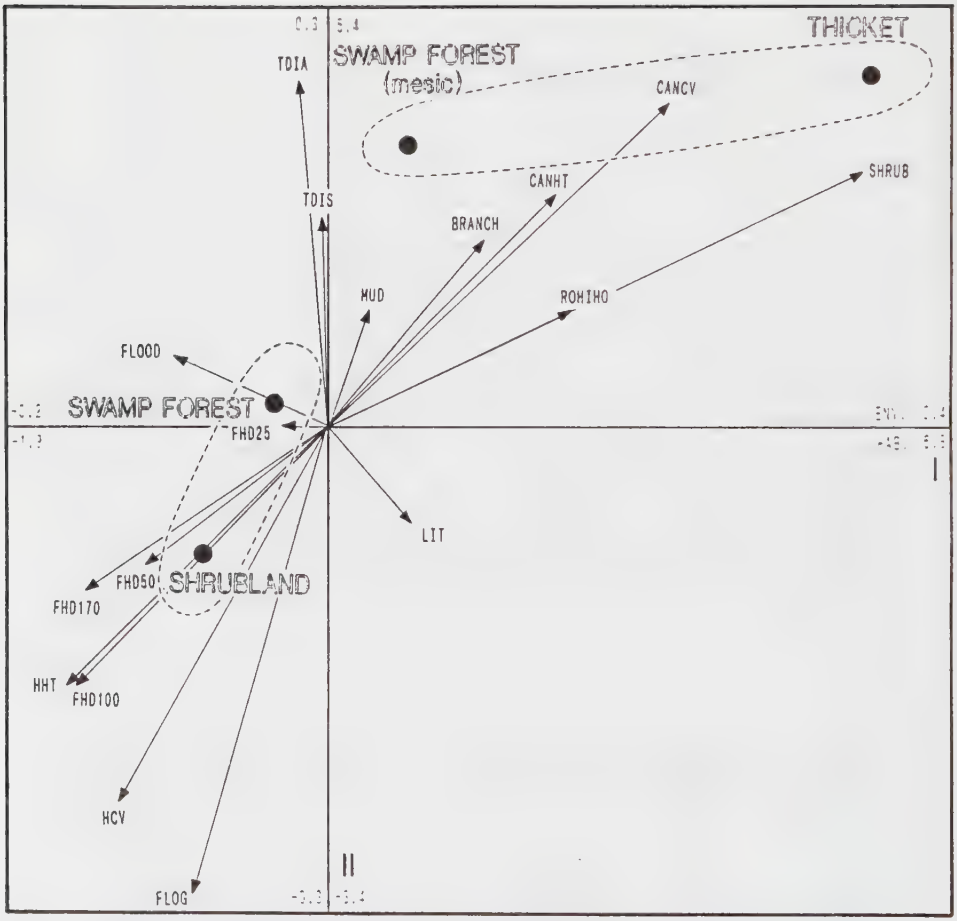


Fig. 44. Canonical Correspondence Analysis (CCA) diagram with habitat centroids on the first two axis (55 trap sites). The centroids are the mean scores of the CCA which are linear combination of environmental variables. The dotted lines delimit the two groups whose Euclidean distance between the centroids is less than the mean ($\overline{d_{jk}}$) of the distance matrix. The environmental variable acronyms are from Tab. 1.

The canonical coefficients and the correlations of the environmental variables with the axis (Tab. 28) show that the first axis (Tab. 29) may be attained as a gradient from sites with high shrub density and high canopy cover (thicket) to those with high herb layer and high foliage height density (shrubland). Both extremes are secondary formations resulting from logging and farming. The first habitat type is the closest to the forest features and the second with low shrub density is highly herb-structured that approximates to grassland characteristics. The variables TDIA, mean trunk diameter, and TDIS, tree dispersion, are more correlated with the second axis showing differences between the two forest habitat types. The swamp forest is less related to the first two axis and, therefore, also to the variables set that is highly correlated with them (Tab. 28). However, it is related to the third axis, that is a moisture gradient (Fig. 45) on which the drier sites have high foliage height density and high relative importance of litter. Along this axis the swamp forest is clearly separated from mesic habitat types. Despite the great differences in the plant species composition, as noted by LINDEMAN et al. (1975), the swamp forest always clustered ($d_{jk}<\overline{d_{jk}}$) with the shrubland mainly due to the herb layer cover and foliage height density. The forest site that clustered with the thicket presents mesic conditions certainly due to artificial drain canals that attenuated its swampy features. However, the topography of the lagoonal terrace is not homogeneous in the region and probably in the pristine condition, it could be originally more mesic in relation to the other swamp forest sites

The forest centroids lie at the right-hand of the diagram showing that both forest types presented herb cover, herbaceous height and foliage height density lower than the shrubland. Nevertheless, in the swamp forest the herb layer is an important structural feature and is more patchy than in other habitat types.

	Canonical coefficients				Correlation coefficients			
AXIS	1	2	3	4	1	2	3	4
variable								
HHT	0.04	0.03	-0.03	0.02	-0.22	-0.18	-0.10	-0.01
HCV*	0.11	-0.09	-0.01	-0.04	-0.18	-0.26	0.12	-0.01
FHD25	0.02	0.04	0.08	0.02	-0.03	0.00	0.18	0.19
FHD50	0.02	-0.03	-0.13	-0.05	-0.16	-0.10	0.16	0.14
FHD100	-0.03	-0.03	0.14	0.08	-0.22	-0.18	0.23	0.16
FHD170	-0.04	0.06	-0.06	0.02	-0.21	-0.11	0.17	0.18
CANHT	0.06	-0.05	-0.06	0.01	0.19	0.17	-0.27	0.03
CANCV	0.09	-0.02	0.01	0.02	0.29	0.23	-0.13	0.06
TDIA*	-0.05	0.07	0.04	-0.01	-0.03	0.25	-0.09	-0.08
TDIS	-0.06	0.01	0.03	0.00	-0.01	0.15	-0.18	-0.04
BRANCH	0.04	0.01	-0.04	0.03	0.13	0.14	-0.26	0.10
FLOG	-0.01	-0.07	0.02	0.00	-0.12	-0.33	-0.01	0.07
SHRUB*	0.05	0.02	0.01	0.01	0.45	0.18	0.10	0.04
ROHIHO*	0.08	-0.02	0.00	-0.02	0.20	0.08	-0.09	-0.11
LIT	0.01	-0.03	-0.02	0.03	0.07	-0.06	0.25	0.11
MUD	-0.04	0.01	-0.02	0.01	0.03	0.08	-0.28	0.09
FLOOD	-0.03	-0.01	-0.04	0.01	-0.13	0.05	-0.31	-0.03

Table 28. Canonical coefficients and intra-set correlations of environmental variables with the first four axis of Canonical Correspondence Analysis (CCA) for the Faxinal data. The environmental variables were standardized to unit variance after log-transformation. Variable acronyms are from Tab. 1. * = variables with t-value <0.05.

	AXIS			
	1	2	3	4
Eigenvalue	0.36	0.25	0.21	0.09
% Var. acc. for	39.26	28.12	22.84	9.78
Cum. % var. acc.	39.26	67.38	90.22	100.00

Table 29. Faxinal region. Eigenvalue, percentage of total variance, and cumulative percentage attributable to each axis in the Canonical Correspondence Analysis (CCA).

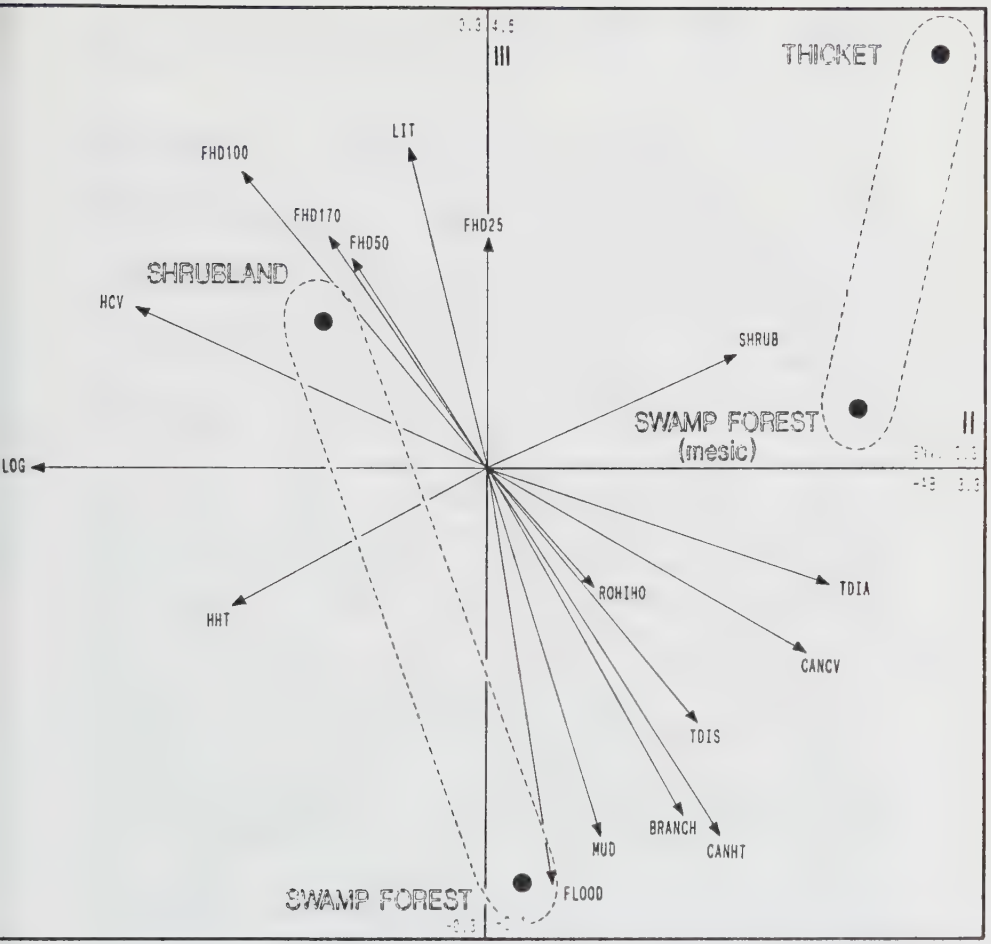


Fig. 45. Canonical Correspondence Analysis (CCA) diagram with habitat centroids (Faxinal region) on the second and the third axis (55 trap sites). The centroids are the mean scores of the CCA which are linear combination of environmental variables. The dotted lines delimit the two groups whose Euclidean distance between the centroids is less than the mean ($\overline{d_{jk}}$) of the distance matrix. The acronyms are from Tab. 1.

2.3.3. RODENTS HABITAT USE

The total capture of rodents (CI_{tot}) in the surveyed habitats increased from the Butiá savanna to the swamp forest and shrubland (Tab. 30). In the latters the index of captures were higher and almost similar, suggesting that they are the most suitable habitats in the region.

The three species *A. nigrita B. lasiurus* and *O. ratticeps* were excluded from some analysis, as the replicated goodness-of-fit test, because of small sample sizes and conclusions concerning their response to different habitat types would be unwarranted.

The replicated goodness-of-fit test pooling the captures of *A. cursor, O. iheringi* and *O. nigripes* was significant (G_p=57.80, d.f.=4, P<0.001), indicating that the rodent community as a whole occurred in microhabitats in frequencies different from their availabilities; the swamp forest and shrubland were favored (Fig. 46.a). The thicket and the Butiá savanna were negatively selected. The analysis including all the habitat types showed some trends in the frequencies of captures between the vegetation zones. The heterogeneity G was not significant (G_H=13.49, d.f.=8, 0.10>P>0.05) and suggests that the rodent community uses the habitats in a homogeneous manner. However, when the Butiá savanna was excluded from the analysis there were evidences that the captures deviate from those expected in a heterogeneous manner (G_H=12.80, d.f.=6, P<0.05). Thus the Butiá savanna avoidance is common to all the species included in the analysis and such trend may be greater than the selection of the secondary growth habitat types. The total G (G_T=71.91, d.f.=12, P<0.001), partitioned into its additive component parts (e.g. the three individual

	SPF	MSF	TKT	SBL	BTS	Totals
A. cursor	35	12	1	17	1	66
	(10.8)	(3.7)	(0.5)	(7.9)	(0.5)	
O. iheringi	2	6	2	4		14
	(0.6)	(1.9)	(0.9)	(1.9)		
A. nigrita				3		3
				(1.1)		
B. lasiurus					1	1
					(0.5)	
O. nigripes	6	2		5		13
	(1.9)	(0.6)		(2.3)		
O. ratticeps		2	2			4
		(0.6)	(0.9)			
NSC	3	4	3	4	2	
Totals	43	22	5	29	2	101
CItot	(13.3)	(6.8)	(2.3)	(13.4)	(0.9)	
Trap-days	324	324	216	216	216	1296

Table 30. Number of captures of each species by habitat category (Faxinal region). Three species, *A. nigrita*, *B. lasiurus*, and *O. ratticeps* were excluded from the replicated goodness-of-fit test because of small sample sizes. In parentheses, the capture index CI (%) based on trapdays *per* habitat. SPF= swamp forest; MSF= mesic swamp forest; TKT = thicket; SBL = shrubland; BTS = Butiá savanna; NSC = number of species caught.

species), showed that only *O. iheringi* (G_{adj}=7.40, d.f.=4, 0.10>P>0.05) appears to be more generalist (Fig. 46.c) at least with regard to the habitat categories analysed. However, the low number of captures suggests prudence in the interpretation of the results. This species is

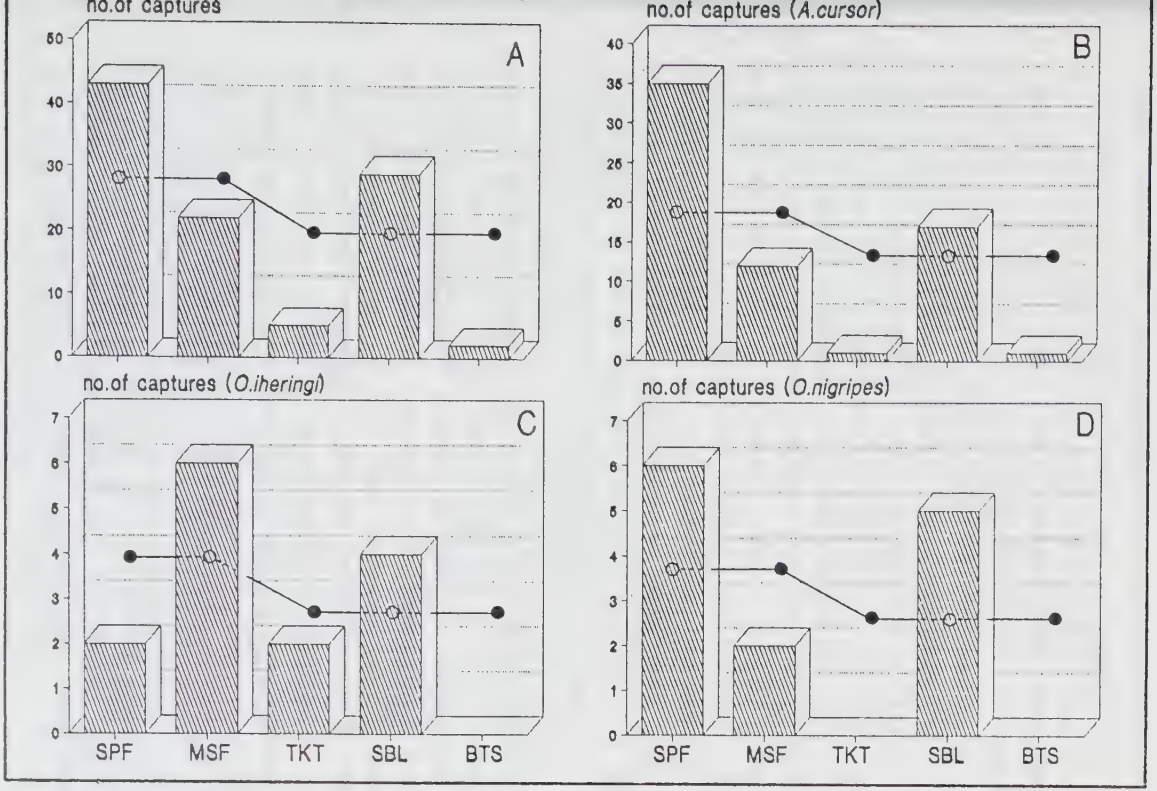


Fig. 46. Observed (solid blocks) and expected (circles) number of captures: pooled (A), *A. cursor* (B), *O. iheringi* (C), and *O. nigripes* (D), in five habitat types in the Faxinal region (cf. Tab. 30). SPF = swamp forest; MSF = Mesic swamp forest; TKT = thicket; SBL = shrubland; BTS = Butiá savanna.

normally associated with forests in southern Brazil and northeastern Argentina (HENSEL, 1872; MASSOIA, 1963), and is able to use secondary formations. The mesic swamp forest sites appear to be more suitable to this species. The captures of *A. cursor* and *O. nigripes* differed from the expected (G_{adj}=49.46, G=12.79, d.f.=4, P<0.05, respectively) within the habitats. *A. cursor* is normally associated with forests and transitional microhabitats (MASSOIA and FORNES, 1962; XIMENEZ and LANGGUTH, 1970; CRESPO, 1982). In the slopes of the south-brazilian highlands, in the secondary formations of the subtropical forest in Rio Grande do Sul, the species is numerically dominant (pers. obs.) and presents higher density than in the primary forest. In the Faxinal region (Fig. 46.b) the captures were more abundant than expected in the swamp forest and in the shrubland. All other habitats appeared to be used with some restrictions. *O. nigripes* inhabits tropical and subtropical forests and areas of secondary growth in southern and eastern Brazil, northeast Argentina and Paraguay (DAVIS, 1947; MASSOIA, 1963; MYERS & WETZEL, 1979, CRESPO, 1982). The captures of this species in the swamp forest and in the shrubland (Fig. 46.d) were higher than expected. The mesic swamp forest appears to be inhabited with some restriction and no capture was obtained in the thicket and in the Butiá savanna. *O. ratticeps* was trapped in the mesic swamp forest and in the thicket. The single capture of *B. lasiurus* was made in the Butiá savanna in a site with low herb cover and almost without litter on the sandy soil. This habitat appears to be the less suitable for all other species known in this region.

The rodent community as a whole do not occur in frequencies different as expected from the habitat availabilities (Fig. 47.a) regarding the forest and the

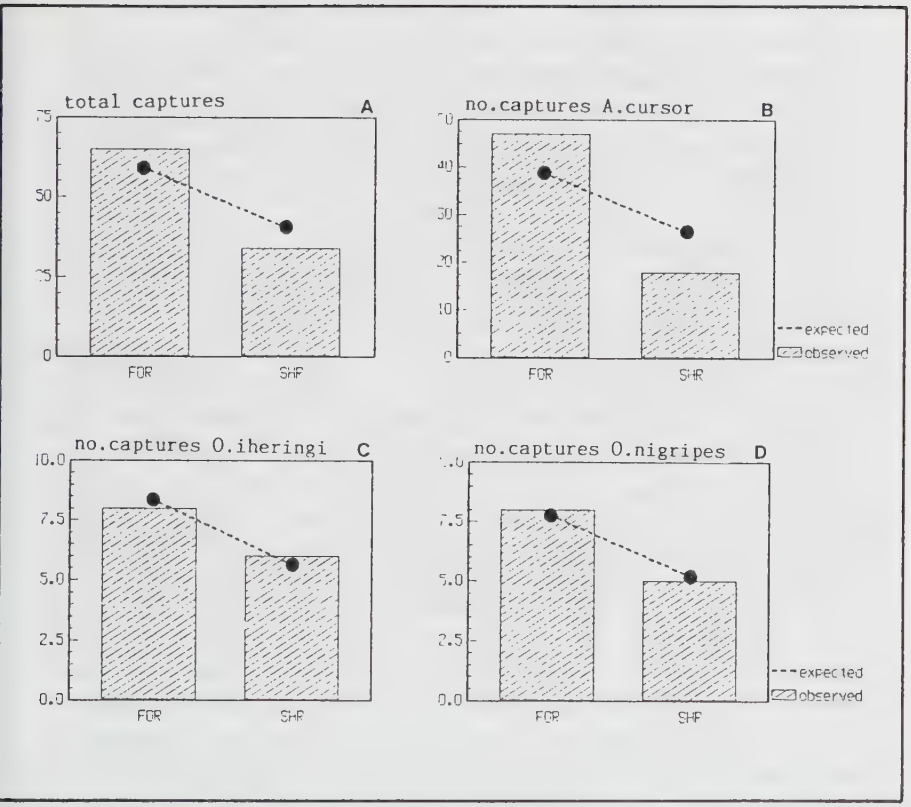


Fig. 47 Observed (solid blocks) and expected (circles) number of pooled captures (A), *A. cursor* (B), *O. iheringi* (C), and *O. nigripes* (D) in two major habitat types (forests -FOR, and shrubland - SHR) in the Faxinal region.

secondary growth formations (G_p=2.82, d.f.=1, 0.10>P>0.05). However, the frequencies differ if the Butiá savanna is included in the analysis (G_p=28.71, d.f.=2, P<0.01). This suggests that areas of secondary growth originated from the same original habitat matrix - the pristine lowland swamp forest - are more suitable than the Butiá savanna that is related to the original zonation. All species included in the analysis deviated from the expected captures in a homogeneous manner (G_{adj}=1.52, d.f=2, P>0.25) showing similar responses in relation to the primary and secondary formations. The total G (G_T=4.36, d.f.=3, P>0.10), partitioned into its additive components, suggests that *A. cursor* (Fig. 47.b) presents some habitat preference (G_{adj}=4.27, d.f.=1, P<0.05). The captures in the forest were greater than expected and the shrubland appeared as a secondary habitat. The captures of *O. iheringi* (Fig. 47.c) and *O. nigripes* (Fig. 47.d) do not differ from the expected in the two habitat types (G_{adj}=0.05, G=0.01, d.f.=1, P>0.10). This indicates that the primary and secondary formations are not differently discriminated by them.

2.3.4. SPECIES / HABITAT STRUCTURE RELATIONSHIPS

In a bivariate correlation analysis with the mean values of the structural variables *per* habitat, no variable was satisfactory (P>0.10) as indicator of the number of species (NSC) and of the number of captures (CI_{tot}).

Among the seventeen environmental variables measured, five of them (HCV, ROHIHO, TRCOS, ARB, DIAMA) fitted very well to the species data (t-tests, all $P<0.05$) contributing significantly to the multiple regression performed by the CCA explaining the observed variations almost equally well as the full set. This variable subset showed different relations regarding the remaining set (APPENDIX 4). The herbaceous cover is largely determined by the canopy cover ($r^2=-0.760$, $P<0.001$), that certainly is the main reason for the structural differences observed between secondary and primary formations. Since extensive areas in the swamp forest are covered by hygrophilous species, a low relation between the herbaceous cover and relative importance of mud (MUD) and relative importance of flood (FLOOD), was observed ($r^2=-0.156$, $r^2=-0.129$, $P<0.01$, MUD and FLOOD respectively). The relative importance of potential rodents "hiding holes" (tree roots and cavities) is negatively related to herbaceous cover ($r=-0.665$, $P<0.001$), that presented higher values in the shrubland. The former variable is positively related with sites with high canopy cover ($r=0.545$, $P<0.001$) and with swampy features ($r=0.511$, $P<0.001$). Its importance increases with tree aggregation ($r=0.651$, $P<0.001$), tree diameter ($r=0.597$, $P<0.001$), and canopy height ($r=0.601$, $P<0.001$). The variables set related to FLOG, fallen logs importance, clearly characterizes the primary swamp forest. This variable was common to all the habitats resulted mainly from logging, except for the swamp forest, where little evidence of such activity was found. It was significantly correlated with FLOOD ($r=0.289$, $P<0.05$), suggesting that the natural fall of trees is a common event in swampy areas, affecting the forest floor features.

The first and the second axis of the canonical ordination (Fig. 48) accounted for 67.38% of the total

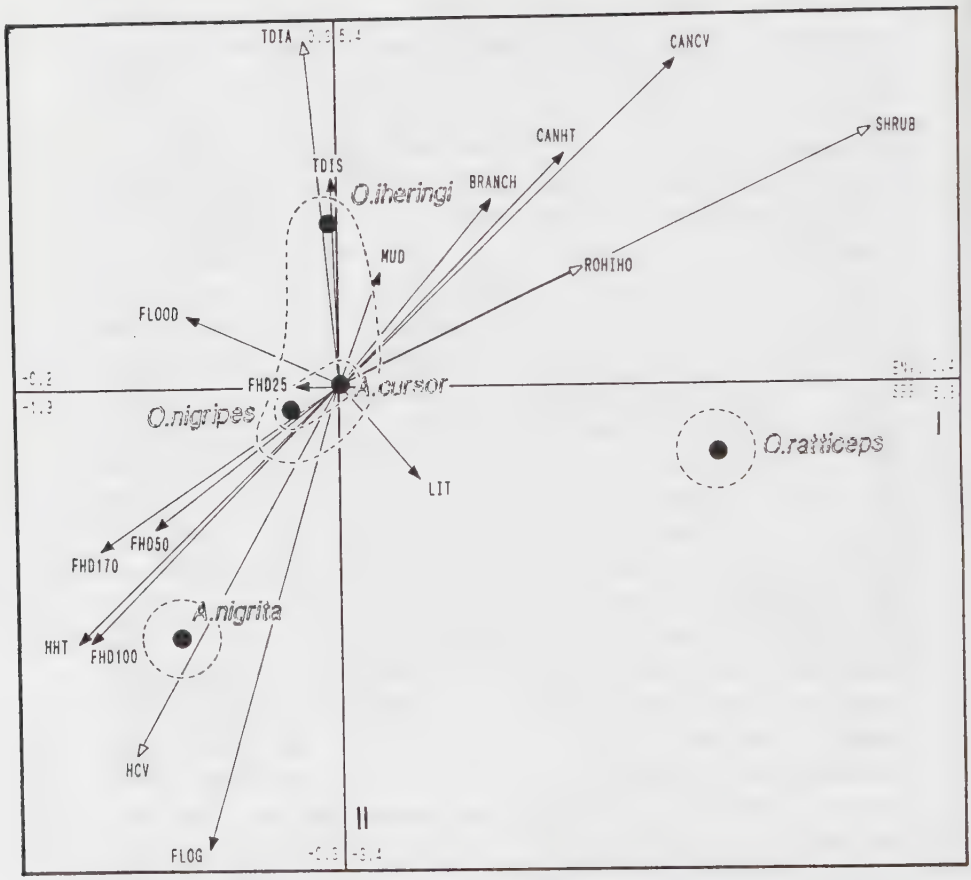


Fig. 48. Ordination diagram (first and second axis) based on Canonical Correspondence Analysis (CCA) of rodent species data with respect to microhabitat structure (for total species caught see Tab. 30). The dotted lines delimit the three groups whose Euclidean distance between the centroids is less than $\overline{d_{jk}}$ of CCA scores. The open arrows are the variables that explains the species data almost equally well as the full set (t-value <0.05). The environmental variable acronyms are from Tab. 1.

variation observed in the capture data (Tab. 29). The first axis (λ_1=0.36) is seen to separate the species related to the shrublands from those with more general distribution or more related to forest sites. However, the first eigenvalue was not significant (MCPtλ_1, P=0.35). It suggests that the separation of the species is not perfect, since some of them are more centered in the diagram. As a consequence the relation between the rodent assemblage and the variables set along the relative chronosequence is not significant. A similar analysis including the Butiá savanna leads to a significant first eigenvalue (MCPtλ_1, P=0.02) showing that the original vegetation zones (Butiá savanna in the high sandy terrace and swamp forest in the lower lagoonal terrace or its secondary stages) are more discriminated by the species than the secondary and more recent habitat types, as the shrublands. The rain forest (not included in this work), presented mesic conditions. Certainly it is differently structured and its microhabitat features may affect the rodent fauna. Nevertheless, at present there are no surveys made in this formation.

The degree of similarity between the species (d_{jk}) in relation to the first and the second axis (Tab. 31) revealed three groups resulting from the cluster analysis of the distance matrix of the species CCA scores. *O. ratticeps* and *A. nigrita* grouped alone (Fig. 48). The centroid of *O. ratticeps* lies at the right-hand of the diagram showing a negative association with sites with high foliage height density up to 170 cm high, high herb layer and high ground cover. This contrasts with *A. nigrita*, whose centroid lies at the lower left corner of the diagram, thus being highly correlated with such variables set. *A. nigrita* presents some semi-fossorial features (MASSOIA, 1962, 1963), makes runways and tunnels under the forest litter, logs, tree roots, and in soft

	AXIS			
	1	2	3	4
A. cursor	-0.06	-0.11	-0.50	0.15
A. nigrita	-1.82	-2.71	2.54	1.44
O. iheringi	-0.12	1.68	0.98	0.26
O. ratticeps	4.07	-0.80	0.94	-0.08
O. nigripes	-0.59	-0.36	0.53	-1.35

Table 31. Species scores on four ordination Canonical Correspondence Analysis (CCA) axis for the Faxinal data.

earth (ALHO, 1982). This species is normally associated with sites with fallen logs (DAVIS, 1947; MYERS & WETZEL, 1979) and those with dense litter as showed in the diagrams (Fig. 49), where the separation from other species is clear. The third group was more centered in relation to the first two axis (Fig. 48) and showed the lowest weight average regarding the total environmental variables set. However, within this group *O. iheringi*, the species more dissimilar, showed some relations to forest or shrubland sites with low-developed herb layer.

No partial canonical correspondence analysis carried out fitting subsets of variables as covariables like those related to the "drain conditions" or to the herb layer features was significant ($P>0.10$). This indicates a low relation between the environmental variables and the rodent assemblage along the relative chronosequence.

The effect of complete disturbance in large areas in the forest and their conversion to agricultural crop land or grazing areas varied within different habitat types. The result of such activity was the increment in the landscape heterogeneity that leads, after abandoning of fields, to a complex of successions and natural zones that

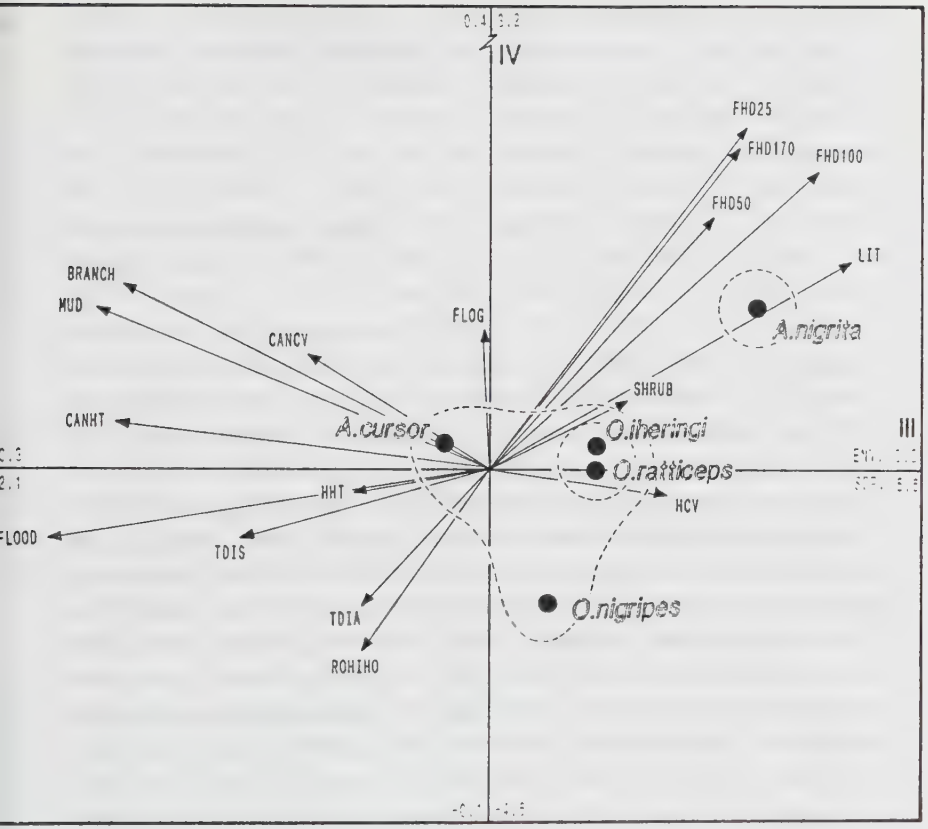


Fig. 49. Ordination diagram (third and fourth axis) based on Canonical Correspondence Analysis (CCA) of rodent species data (Faxinal region) with respect to microhabitat structure (for total species caught see Tab. 30). The dotted lines delimit the three groups whose Euclidean distance between the centroids is less than $\overline{d_{jk}}$ of CCA scores. The open arrows are the variables that explains the species data almost equally well as the full set (t-value < 0.05). The environmental variable acronyms are from Tab. 1.

persisted as relicts. However, the success of rodent colonization or persistence in secondary habitats depends primarily on the microhabitat features. The abandoning of fields in the lower lagoonal terrace resulted in extensive secondary growth vegetation which is composed of arborescent shrubs (*Baccharis sp.*) and in some places of dense herb layer. These shrublands are apparently persistent (LINDEMAN et al., 1975) and an equilibrium stage may be reached with the prevalence of some major species instead of a continuous change toward the swamp forest traits. Despite the great differences between several microhabitat analysed along the relative chronosequence, the rodent community as a whole was not related to the different sets of environmental variables sets that described the microhabitat structural features. This could be an evidence that successional changes in vegetation do not necessarily cause significant responses from mammal communities as some times suggested (MacMAHON, 1981; HUNTLY and INOUYE, 1987). On the other hand, the lack of significant relations between rodents and the microhabitat features may be a consequence of the shrubland persistence. However, this speculation requires further investigations.

2.4. COSTA DE DENTRO (Santa Catarina Island)

2.4.1. OVERALL HABITAT STRUCTURAL SIMILARITIES

In the South of the Santa Catarina Island the complex of habitat surveyed revealed three groups of similarity ($d_{jk}<\overline{d_{jk}}$) ($r_{cd}=0.867$, $P<0.01$) concerning their general structural features (Tab. 32). In some cases despite the different composition and origins (Fig 50), some habitat types (e.g. sand forest and shrubland) were grouped together showing some structural relations. The shrubland for example, resulted from intensive logging in the rain forest on the slopes (50-150 m a.s.l.) of the granitic Serra do Mar, whereas the Restinga forest is located on a Holocene marine sandy terrace. The latter habitat type is remnant from a more extensive formation on the sandy terrace and it seems likely that its actual structural features were largely determined by human disturbance. The primary rain forest on the hill slopes composed a similarity group with its structural variant, the disturbed rain forest, that resulted from a relative man-made disturbance. In the latter only some large trees were removed and apparently a complet disruption of the forest structure as observed in the shrubland areas did not occur. The swamp forest was more related to the Maricá woodland and to the stream edge habitat type. Patches with high herb layer and dense ground cover are common features of this habitat type. Swampy sites may be frequent but during the study period such area was relatively dry. The

Habitat Variable	SPF	RFO	DRF	SBL	MWL	SDF	STE	GSW
HHT	108.79	29.64	39.72	56.23	79.69	44.22	89.57	136.34
HCV	65.34	31.47	28.01	66.24	71.00	60.07	47.68	96.73
FHD25	3.99	5.41	4.18	9.74	4.50	5.00	4.38	18.96
FHD50	10.68	10.94	10.00	23.75	14.02	13.84	10.77	41.09
FHD100	29.47	16.67	19.54	39.34	33.32	31.85	25.35	72.77
FHD170	67.52	21.26	23.14	53.16	49.18	69.93	41.23	78.61
CANHT	7.55	10.12	9.24	3.85	7.34	2.59	8.15	0.00
CANCV	69.33	88.38	88.42	25.95	32.96	24.78	59.20	2.50
TDIA	19.63	25.39	28.62	0.00	31.13	0.00	27.91	0.00
TDIS	1.35	2.01	1.21	0.13	1.09	0.17	1.08	0.05
BRANCH	2.93	5.67	4.03	0.00	0.36	0.00	1.05	0.00
FLOG	16.10	24.31	67.67	3.50	0.00	3.00	6.76	0.00
SHRUB	7.44	16.00	22.67	37.50	3.20	14.25	5.97	3.50
ROHIHO	10.86	3.13	0.50	0.00	2.60	1.25	1.69	0.00
LIT	5.00	5.91	3.23	2.80	1.27	3.35	2.45	0.27
MUD	0.00	0.00	0.00	0.00	0.00	0.00	1.50	27.00
FLOOD	0.00	0.00	0.00	0.00	0.00	0.00	1.00	47.50
ROCK	0.00	27.00	24.00	22.00	0.00	0.00	17.50	0.00
ROCAV	0.00	7.25	1.33	0.33	0.00	0.00	0.75	0.00
SLOPE	0.00	26.00	22.00	13.50	0.00	0.00	10.00	0.00

Table 32. Costa de Dentro. Sample estimates of the mean for twenty habitat variables for each habitat type. The acronyms are from Tab. 1. SPF = swamp forest; RFO= rain forest; DRF= degradated rain forest; SBL= shrubland; MWL= Maricá woodland; SDF= sand forest; STE= Stream edge; GSW= grassy swamp.

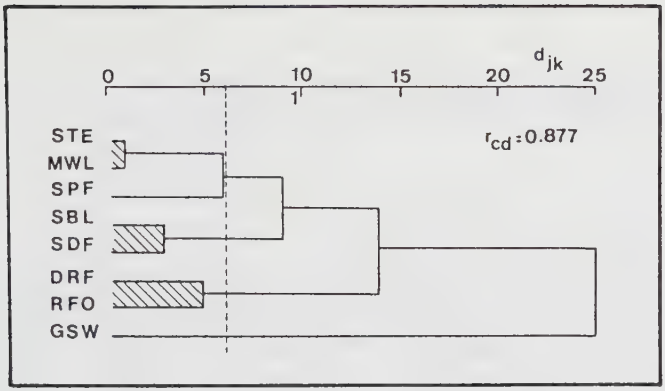


Fig. 50. Costa de Dentro. Dendrogram of habitats structural relationships. d_{jk} = structural distance (Euclidean distance - rescaled). The dashed line represents the mean Euclidean distance ($\overline{d_{jk}}$). The diagonal shading area demarcate the groups with high structural similarity (d_{jk}-s). STE= Stream edge; MWL= Maricá woodland; SPF = swamp forest; SBL= shrubland; SDF= sand forest; DRF= degradated rain forest; RFO= rain forest; GSW= grassy swamp. r_{cd}=cophenetic correlation.

stream edge is a complex area and is related to the swamp and the rain forest. However, in the flat lands *Mimosa bimucronata* (LEGUMINOSAE) is largely dominant and determines the woodland structure.

Among the habitats surveyed only the extensive grassy marsh (Pantano do Sul) composed a separated group differing from the others mainly with the swampy, grassy, and treeless traits. This habitat type is located on the Holocene lagoonal and bay-bottom deposits (SUGUIO et al., 1986) that compose a large and flat area bordered in East and West sides by granitic hills. Holocene marine sandy terraces delimit the north and the southern edge near the Ocean.

2.4.2. HABITAT GRADIENTS

The canonical coefficients and the correlations of the environmental variables with the CCA axis showed that the first axis represents a sharp variation from the grassy swamp to the forest or the shrubland sites. Since the relatively high similarity between these habitats contrasts with the low relation shown by all of them with the grassy swamp, they were grouped together difficulting the comparative analysis of the structural similarities. A further canonical ordination excluding the grassy swamp showed that the first axis (λ_1= 0.49) is a forest canopy height, canopy cover, and tree diameter gradient (Tab. 33) ranging from the sand forest sites to the swamp forest and the rain forest situated near or on the granitic hill slopes.

The differences between the habitat groups in relation to the variables set are shown by the second and the third ordination axis that accounted for 58.84% of the total observed variation (Tab. 34). The mean scores which are linear combination of environmental variables (TER BRAAK, 1986) resulting from the CCA showed three similarity groups ($d_{jk}<\overline{d_{jk}}$) by the cluster analysis of the Euclidean distance matrix (Tab. 35). These groups are largely separated in relation to both axis (Fig. 51). A high cophenetic correlation was observed (r_{cd}=0.944, P<0.001).

The two groups more related to the second axis: stream edge and those habitats with shruby features (shrubland, Maricá woodland, and sand forest) are largely separated. They characterize a habitat set with low similarity to the

	Canonical coefficients				Correlation coefficients			
AXIS	1	2	3	4	1	2	3	4
variable								
HHT	-0.03	0.00	0.01	-0.00	-0.03	0.07	-0.01	-0.08
HCV	-0.03	0.01	-0.03	-0.00	0.13	-0.06	0.14	0.15
FHD25	-0.02	0.04	-0.06	-0-01	-0.13	0.14	0.11	0.20
FHD50	-0.05	0.00	0.06	-0.02	-0.12	-0.09	0.25	0.30
FHD100	-0.08	-0.08	0.04	0.08	0.05	-0.19	0.16	0.32
FHD170*	0.13	0.08	-0.08	-0.04	0.29	-0.06	0.02	0.06
CANHT	0.00	-0.01	0.04	-0.01	-0.34	0.12	-0.28	0.18
CANCV	-0.08	0.06	-0.06	0.03	-0.31	0.11	-0.42	-0.02
TDIA*	-0.07	0.00	-0.01	-0.02	-0.37	0.13	-0.08	-0.09
TDIS	-0.03	0.02	-0.01	-0.02	-0.33	0.10	-0.23	-0.18
BRANCH	0.01	-0.01	0.00	-0.02	-0.17	0.06	-0.23	-0.06
FLOG	0.01	-0.01	-0.03	-0.01	-0.19	0.00	-0.43	0.13
SHRUB	-0.05	-0.04	0.02	-0.02	-0.02	-0.20	0.16	-0.04
ROHIHO*	-0.06	0.01	0.01	0.02	-0.18	0.16	-0.08	-0.09
LIT	-0.01	-0.04	0.03	-0.01	-0.06	-0.04	-0.15	-0.01
MUD	0.01	0.01	-0.02	0.00	0.00	0.33	0.14	0.06
FLOOD*	0.02	0.08	0.05	0.03	0.07	0.56	0.31	0.20
ROCK	-0.01	0.03	-0.01	-0.03	-0.12	0.01	-0.15	0.14
ROCAV*	0.02	-0.02	-0.04	0.06	-0.14	-0.04	-0.32	0.45
SLOPE	0.05	0.03	-0.02	0.03	-0.17	-0.08	-0.18	0.19

Table 33. Canonical coeficients and intra-set correlations of environmental variables with the first four CCA axis for Costa de Dentro data. The environmental variables were standardized to unit variance after log-transformation. Variable acronyms are from Tab. 1.

	AXIS			
	1	2	3	4
Eigenvalue	0.49	0.42	0.31	0.18
% Var. acc. for	31.67	27.17	20.15	11.79
Cum. % var. acc.	31.67	58.84	78.99	90.78

Table 34. Costa de Dentro. Eigenvalue, percentage of total variance, and cumulative percentage attributable to each axis in the Canonical Correspondence Analysis (CCA).

	SPF	RFO	DRF	SBL	MWL	SDF	STE
SPF	0.00						
RFO	1.08	0.00					
DRF	0.69	0.41	0.00				
SBL	2.60	2.30	2.45	0.00			
MWD	2.50	2.40	2.47	0.47	0.00		
SDF	2.20	1.76	1.95	0.56	0.85	0.00	
STE	1.54	2.47	2.16	2.73	2.38	2.62	0.00

$\overline{d_{jk}}$=1.84

s=0.81

Table 35. Euclidean distance (d_{jk}) between the habitat centroids on the second and third axis. SPF = swamp forest; RFO= rain forest; DRF= degradated rain forest; SBL= shrubland; MWL= Maricá woodland; SDF= sand forest; STE= stream edge; GSW= grassy swamp.

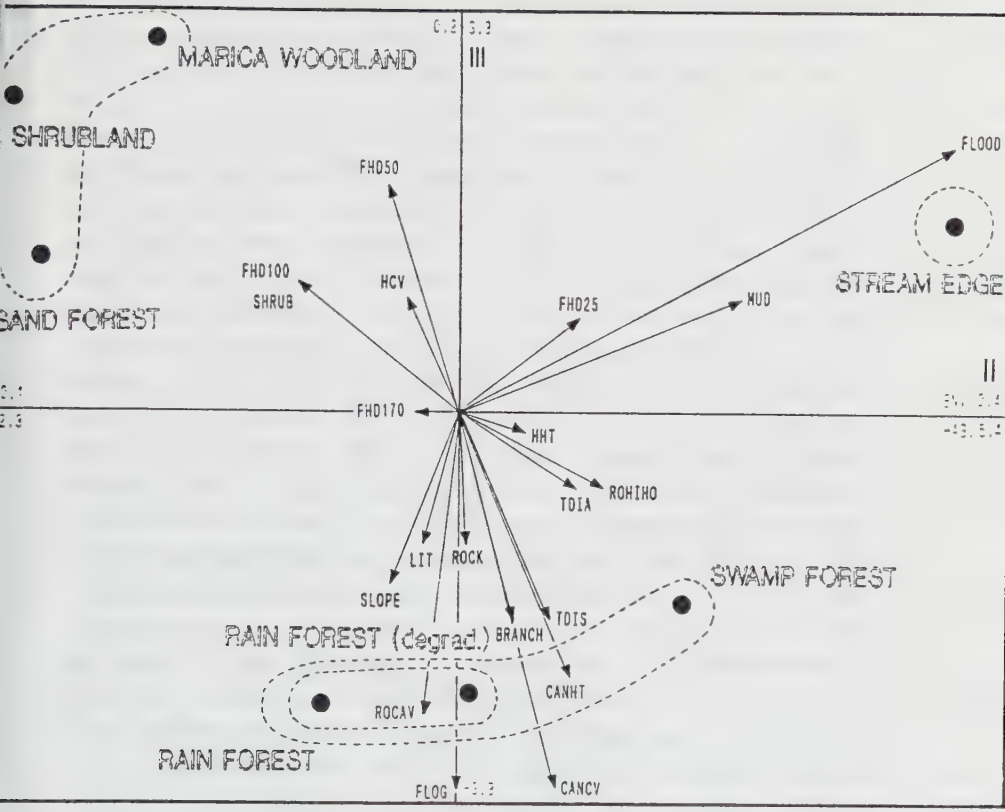


Fig. 51. Canonical Correspondence Analysis (CCA) diagram with habitat centroids (Costa de Dentro) on the second and the third axis (51 trap sites). The centroids are the mean scores which are linear combination of environmental variables. The dotted lines delimit the three groups whose Euclidean distance between the centroids is less than the mean ($\overline{d_{jk}}$) of the distance matrix (cf. Tab. 35). The environmental variable acronyms are from Tab. 1.

forests. Both are extremes of a gradient represented on the third axis, that ranges from sites with low canopy cover and high foliage height density (up to 1 m high) to those with high canopy cover and lower herb layer importance as represented by the forests. The forest habitats are located at the lower right and left-hand side of the diagram. In this group a subgroup composed of rain forest and its variant (degradated rain forest) is characterized by fallen logs, relative importance of rock cavities, and by the terrain slope, whereas the swamp forest is distinguished by a flat terrain and higher importance of tree root cavities as potential rodents "hiding holes". Both the variables ROHIHO and ROCAV characterize these habitat groups appart from the remaining variables that normally typify the forest habitats and compose their main structure. The shrubland area is negatively correlated with the variable ROCAV that characterizes the more intact sites in the rain forest. This is an evidence that after logging, a substantial transformation in the ground is carried out by removing rocks to favor farming. In this way, such activity could affect the successional changes and consequently the forest features of the partially new substrate.

2.4.3. RODENTS HABITAT USE

In a bivariate correlation analysis with the mean values of the structural variables *per* habitat, no significant correlation with the number of species caught (NSC) was obtained ($P>0.05$). The total capture of rodents (CI_{tot}) was correlated to several variables (Fig. 52), particularly with those related to ground features as

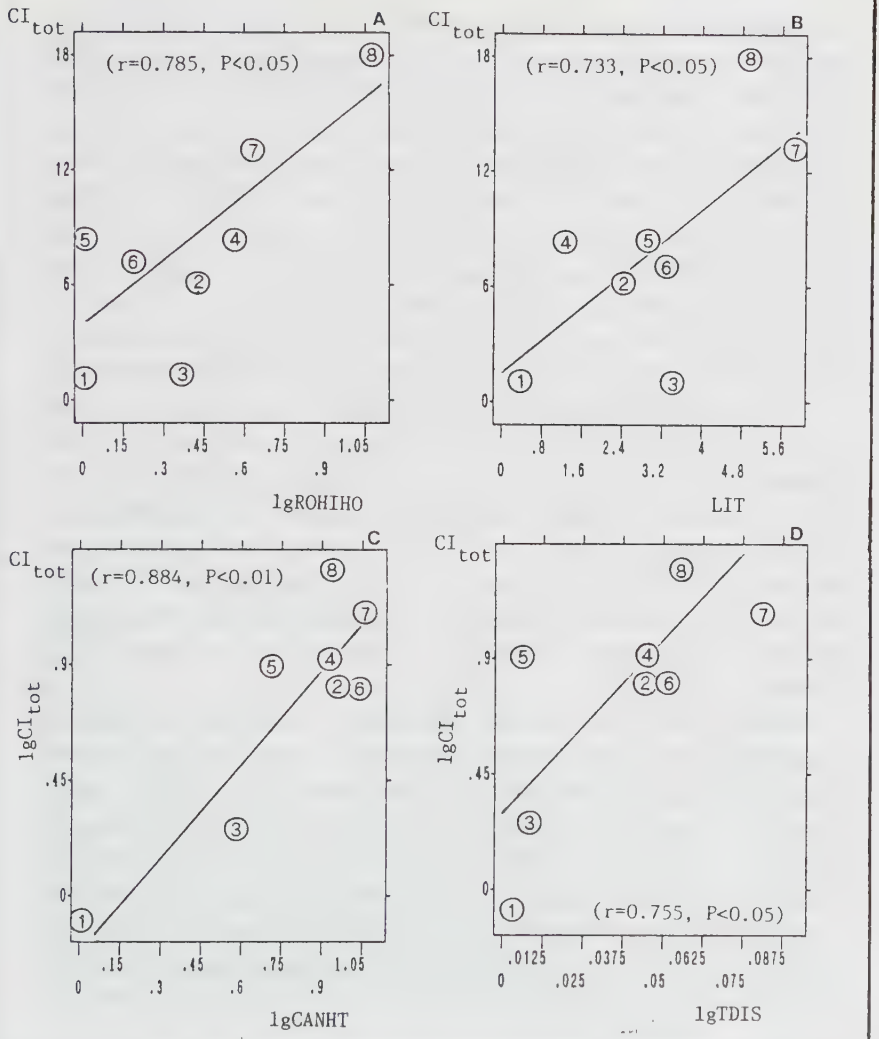


Fig. 52. Relationships between the index of captures (CI_{tot}) and the mean of the relative frequency of potential rodents hiding holes (A), litter soil-depth (B), canopy height (C), and tree dispersion (D) by habitat type. 1. grassy swamp; 2. Stream edge; 3. sand forest; 4. Maricá woodland; 5. shrubland; 6. degradated rain forest; 7. rain forest; 8. swamp forest (cf. Tab. 32 and Tab. 36). The environmental variables in A, C and D were log+1 transformed.

ROHIHO, potential "hiding holes" ($r=0.785$, $P<0.05$); LIT, relative importance of litter ($r=0.733$, $P<0.05$); MUD, relative importance of mud ($r=-0.734$, $P<0.05$); and FLOOD, relative importance of floods ($r=-0.753$, $P<0.05$). Likewise, significant correlations were observed with many variables related to forest features as CANHT, canopy height ($r=0.884$, $P<0.05$), TDIS, tree dispersion ($r=0.755$, $P<0.05$), and CANCV, canopy cover ($r=0.726$, $P<0.05$). Some of these variables, however, are not directly related to the rodent species but indicated that the species are affected by the landscape features. The forests appear to be more suitable habitats whereas the open habitat types or those departing from the forest features are less appropriate for the rodent community. Furthermore, the captures were negatively correlated ($P<0.05$) to FHD50 ($r=-0.716$) and FHD100 ($r=-0.743$), two variables that characterize the herb layer vertical structure. The higher values of these variables were observed in the grassy marsh, the habitat type with lower relative density of rodents.

In a multiple regression analysis by the stepwise procedure no variable was selected to predict the species number with the environmetal variables by habitat type. However, two of them appeared to be satisfactory to the CI_{tot} prediction. The multiple regression equation ($R=0.953$, $P<0.01$) demonstrates that the captures tend to increase with the increment of the relative importance of potential rodents "hiding holes" in tree roots (ROHIHO) and with the frequency of rock cover in the forest ground:

$$CI_{tot} = 1.357 + 0.238\ ROCK + 1.525\ ROHIHO$$

Both variables are important in the rain forest and in the swamp forest near or on the granitic hill slopes. It seems likely that these habitat characteristics influence

significantly the rodent density and may limit their occurrence in the region.

The total capture of rodents (CI_{tot}) in the surveyed habitats was lower in the grassy swamp and in the sand forest (Tab. 38). The higher CI_{tot} was observed in the rain forest and in the swamp forest respectively. *A. cursor* was always numerically dominant and the other species were trapped only in small numbers. The analysis pooling the captures showed that the community as a whole occupied the habitats in frequencies different from their availabilities (G_{adj}=53.32, d.f.=7, P<0.01). The grassy swamp and the sand forest were strongly avoided (Fig. 53.a), whereas the swamp forest and the rain forest were favored. The other habitat types such as the shrubland, Mariçá woodland, stream edge and the degradated rain forest appear to be used in a proportion near to their relative availability. Nevertheless, the low number of captures of several species bounded the analysis, and the numerical dominance of *A. cursor* shaped the community pattern. This species does not use the habitats in proportion to their relative availability (G_{adj}=53.7; d.f.=7, P<0.01). The sand forest and the grassy swamp were negatively selected (Fig. 53.b). The forest habitat types appeared to be more suitable to the species. This observation is consistent with data from other regions (this work; MACDONALD AND FORNES, 1982). Regarding other habitat types the species appears to use all of them in a proportion near their relative availability.

	RFO	DRF	SBL	STE	SPF	MWL	SDF	GSW	TOTAL
O. hispidus			2	1		2	1		6
			(1.7)	(0.4)		(1.7)	(0.4)		
A. cursor	15	8	8	11	20	8	1	1	72
	(12.5)	(6.7)	(6.7)	(4.6)	(16.7)	(6.7)	(0.4)	(0.4)	
N. squamipes				2					2
				(0.8)					
O. nitidus					1				1
					(0.8)				
O. ratticeps	1								1
	(0.8)								
O. flavescens								1	1
								(0.4)	
O. nigripes				1			2		3
				(0.4)			(0.8)		
NSC	2	1	2	4	2	2	3	2	
Totals	16	8	10	15	21	10	4	2	86
CItot	(13.3)	(6.7)	(8.3)	(6.3)	(17.5)	(8.3)	(1.7)	(0.8)	
Trapdays	120	120	120	240	120	120	240	240	1320

Table 36. Costa de Dentro region. Number of captures of each species by habitat category. In parentheses, the capture index CI (%) based on trapdays *per* habitat. SPF = swamp forest; RFO= rain forest; DRF= degradated rain forest; SBL= shrubland; MWL= Maricá woodland; SDF= sand forest; STE= Stream edge; GSW= grassy swamp; NSC = Number of species caught.

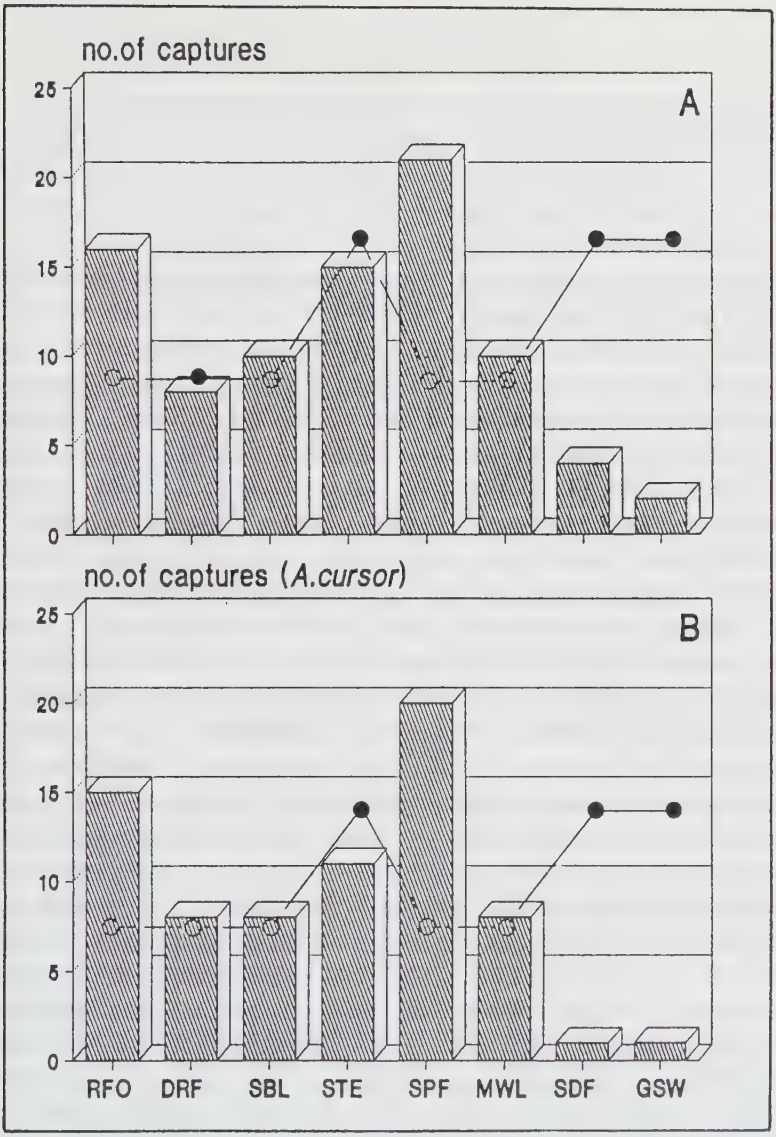


Fig. 53. Observed and expected number of total rodent captures (A) and *A. cursor* (B) in eight habitats in the Costa de Dentro region (cf. Tab. 36). RFO= rain forest; DRF= degradated rain forest; SBL = shrubland; STE = Stream edge; SPF = swamp forest; MWL = Maricá woodland; SDF = sand forest; GSW = grassy swamp. ▨ Observed O—● Expected

2.4.4. SPECIES / HABITAT STRUCTURE RELATIONSHIPS

Among the twenty variables measured at each positive trap site, five of them (Tab. 33) fitted very well to the species data ($P<0.05$). They contributed significantly to the multiple regression in the CCA and constituted a subset of environmental variables that explained equally well the full set of the species-environment biplot. The variable FLOOD is important in habitats on the lower terrace ($t=2.22$, $d.f.=28$, $P<0.05$), as at the stream edge. The variable FHD170, foliage height density up to 170 cm high ($t=2.76$, $d.f.=28$, $P<0.01$) is notable in habitats with low canopy cover as in the forest sites with dense undergrowth. The significance of the variable TDIA, mean tree trunk diameter ($t=2.62$, $d.f.=28$, $P<0.05$), suggests that the distribution of rodents is affected by the forest features. The species respond to the gradient that ranges from secondary vegetation or the sand forest, to those in the primary forest near or on the hill slope. The remaining significant variables (ROHIHO and ROCAV), relative importance of potential rodents "hiding holes" and relative importance of rock cavities ($t=2.16$, $t=2.28$, $d.f.=28$, $P<0.05$, respectively) had significant effect on the rodent distribution since their occurrence and density may be limited at least in part by the relative availability of favorable shelters in the forest floor.

The first and the second axis of the canonical analysis that characterize a gradient related to arboreous strata (CANHT, TDIS, TDIA, CANCV) and a moisture gradient, accounted for 58.84% of the total variation observed in the species-environment biplot (Tab. 34).

The first eigenvalue (λ_1=0.49) was not significant ($MCpt_{\lambda 1}$, P=0.14), implying that the structural differences observed between the microhabitats along the main gradient (forest - shrubland habitat types) do not explain very well the distribution of captures. Likewise, the same result was obtained for the four eigenvalues extracted ($MCpt_{\lambda 1-4}$, P=0.14). Therefore, the rodent community as a whole seems not to be well related to the microhabitat features. The partial Canonical Correspondence Analysis carried out with several environmental variables sets (as those related to the herb layer features or to the drain conditions) as covariables, failed to find significant relation between rodents and the microhabitat structure. This occurs presumably as a result of the gradual variation in the sites. Despite the differences, some of them are originated from the same original matrix and present several common features (Tab. 32, APPENDIX 5) thus resulting in a low discrimination by the rodents. Some habitats are continuous as swamp forests and the rain forests and are not discerned, at least by the numerically dominant species. Nevertheless, in an analysis with the variables set that contributed significantly to the regression in the CCA (t-teste, P<0.05), and excluding the remaining set (Fig. 54), a significant relation between the rodents and the habitat features was observed ($MCpt_{\lambda 1-4}$, P<0.05).

Four groups of species differed by the degree of similarity (d_{jk}) (Tab. 37) in relation to the canonical axis (Tab. 38). *N. squamipes* at the right-hand of the diagram showed high correlation with the relative importance of floods. This semiaquatic rodent is normally found close to water bodies (MOOJEN, 1952; ALHO, 1982; ERNEST, 1986; ALHO et al. 1986). In southern Brazil the species is normally found in gallery forest and in the tropical and subtropical forest on the south brazilian

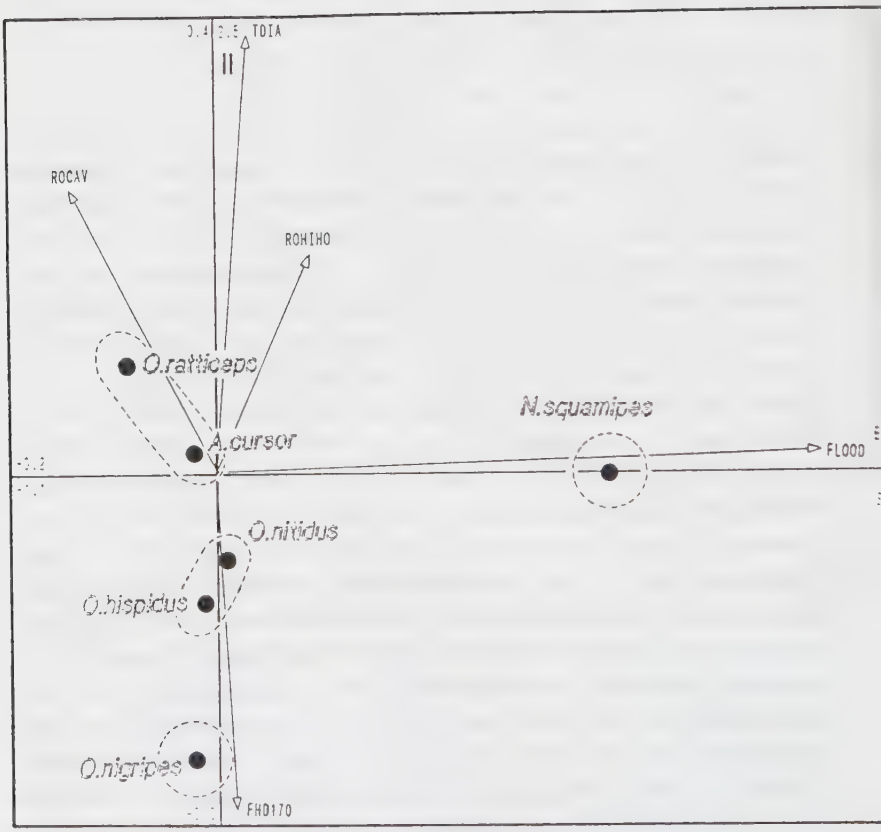


Fig. 54. Ordination diagram based on canonical correspondence analysis (CCA) of the rodent species data (Costa de Dentro) with respect to microhabitat structure (for total species caught see Tab. 36). The dotted lines delimit the four groups whose Euclidean distance between the centroids is less than $\overline{d_{jk}}$ of CCA scores. Only varibles with t-value<0.05 were included. The environmental variable acronyms are from Tab. 1.

	OXYHIS	AKOCUR	ORYRAT	ORYSUB	ORYNIG	NECSQU
OXYHIS	0.00					
AKOCUR	1.10	0.00				
ORYRAT	1.80	0.78				
ORYSUB	0.30	0.84	1.59	0.00		
ORYNIG	1.10	2.20	2.88	1.38	0.00	
NECSQU	2.53	2.35	2.88	2.31	3.14	0.00

d_{jk} = 1.812

s = 0.878

Table 37. Euclidean Distance (d_{jk}) between the species centroids related to first and second axis. OXYHIS = *O. hispidus*; AKOCUR = *A. cursor*; ORYNIG = *O. nigripes*; ORYRAT = *O. ratticeps*; ORYNIT = *O. nitidus*; NECSQU = *N. squamipes*.

	AXIS			
	1	2	3	4
O. hispidus	-0.17	-1.30	-0.32	-0.36
A. cursor	-0.19	0.29	-0.12	0.00
O. ratticeps	-1.05	1.28	5.48	-0.19
O. nitidus	0.11	-0.97	0.14	2.82
O. nigripes	-0.21	-3.06	0.82	-0.01
N. squamipes	4.51	0.10	0.34	-0.07

Table 38. Species scores on four CCA ordination axis for Costa de Dentro data.

highland slopes. The species appears to be absent in the extensive grassy marshes in the Restinga. A second group more centered in the diagram is composed of *A. cursor* and *O. ratticeps*. *A. cursor* is nearest to the center of the diagram which implies low relation with both axis. This observation is consistent with the data from Faxinal in the north of the Coastal Plain of Rio Grande do Sul (this work), where the species was also found in all the surveyed habitats and presented low relation to the four ordination axis extracted by the CCA, thus showing low predictability of the frequency of captures by the environmental variables. *O. ratticeps* was associated to rock cavities (ROCAV) and to the availability of potential "hiding holes" in tree roots (ROHIHO). Despite the low number of captures the record is in aggreement with those from other regions in the coast of Rio Grande do Sul (this work). It seems likely that the occurrence of this large species of *Oryzomys* is related to the forest floor features. The third and fourth groups are negatively related to the second axis suggesting that these species are more related to sites with high foliage height up to 170 cm high, despite their distinct composition. *O. hispidus* was more frequent in the shrubland and in the Maricá woodland. The first habitat type on the hill slopes is composed mainly of shrubs (*Baccharis sp.*) sometimes with interlocked-branches and patches of grasses in more open sites. It contrasts with the second habitat type in the plain, with *M. bimucronata* that may be considered transitional from the grassy swamp to the swamp forest. In this site, the ground layer is highly patchy, sometimes composed of grasses, ferns or clumps of reeds. The single capture of *O. nitidus* was made in the swamp forest in a trap site with dense cover of *Calathea* sp. (MARANTACEAE). *O. nigripes* was trapped in the sand forest with undergrowth composed of bromeliads, and in the stream edge

with *Heliconia sp.* (HELICONIACEAE) and dense clumps of bamboos.

The species ordination is more related to microhabitat features than to the habitat variation. Some species trapped in different habitats are close together concerning the structure of the trap sites. In this way, the data suggest that interactions with the microhabitat structure determine the distribution of the species in the region. However, the lack of significance in the relations between the species and the environmental variables occurred presumably in part as a result of the peculiarity of the habitats surveyed. Part of them compose a similar matrix in the landscape since the forest or shrubland features predominate. If the grassy swamp is included in the analysis the relation is highly significant ($MCpt\lambda_1$, P=0.01), suggesting that the swamps on the lower Holocene lagoonal and bay-bottom deposits are largely disharmonic with the rodent fauna.

3. REMARKS ON THE CRICETID FAUNA IN THE RESTINGA SCENARIO

The extreme South of Brazil is included in a large transitional zone between two major mammalian zoogeographic subregions of South America; the Brazilian Subregion and the Patagonian Subregion (HERSHKOVITZ, 1958). In such transitional zone most of the tropical genera reach their southern limits along a diagonal from northern and central Andes to northeastern Argentina, Uruguay and southern Brazil (HERSHKOVITZ, 1958, 1972). A more recent review of faunal regions, conducted at the family level, recognizes such transitional zone (SMITH, 1983a, 1983b) and includes southern Brazil and Uruguay entirely within the newly-termed Neotropical Subregion. Despite the taxa studied, methodologies, or the taxonomic level employed, and the resulting different boundaries between the subregions, the transitional zones delimited by several authors (MELLO-LEITÃO, 1946; HERSHKOVITZ, 1958, 1972; CABRERA and YEPES, 1960; FITTKAU, 1969; KOOPMAN, 1982) are in close agreement. The diagonal southeastern/northwestern is always observed as an evidence of some ecological discontinuity and that the neotropical biota is subject in such area to diverse ecological constraints. The subdivision of southern Brazil and neighbouring areas into a number of faunal and biogeographic provinces or districts (CABRERA and YEPES, 1960; MELLO-LEITÃO, 1946; CABRERA and WILLINK, 1980) attests the complex interactions between the biota and the major components of the landscape.

The evaluation performed in seventeen areas along the Coastal Plain, and in the south-brazilian highland slopes in Rio Grande do Sul and in the Santa Catarina Island, demonstrated that the rodent fauna is differently composed particularly along the coast. The species composition varies markedly from North to South and West to East as result of a complex interplay of historical and ecological factors. In the lowlands in the northern region, and in the eastern slopes of the Serra do Mar and Serra Geral, the Atlantic Forest is the most extensive plant formation (RAMBO, 1951; VELOSO and KLEIN, 1963; KLEIN, 1978; WAECHTER, 1985). In the central and southern regions open vegetation as grasslands and swamps predominate in the landscape (LINDMAN, 1906; RAMBO, 1954; PFADENHAUER and RAMOS, 1979; PFADENHAUER, 1980; MOHRDIECK, 1980; WAECHTER, 1985). The Restinga rodent fauna composition represents the interface between tropical and subtropical regions. The assemblages on the north portion of the coast showed similarities to those found in the south-brazilian highland slopes, northeasthern Argentina, Paraguay and northern regions of Brazil. Thus the abrupt changes in the topographic features in the extreme north of the coast of Rio Grande do Sul due to the occurrence of the South Brazilian Highlands do not coincide with changes in the rodent fauna composition. The rodent assemblages in the mainland northern Restinga are more tropical. The forest elements are common, some of them occurring in open formations, composed largely of a complex of seral stages resulting due to human disturbances. In the Santa Catarina Island the rodent fauna presents similar pattern. However, the treeless habitats, as the extensive grassy swamps and the sandy grasslands, seem to be less adequated to the rodent assemblage. Important to note is that in this region grassland-species were not found. Such observation

contrasts greatly with other data from southern regions where the assemblages are composed partially of some elements related to forests and others more related to grassland habitat types. The elements commonly found in the south are largely absent in the north of the Coastal Plain of Rio Grande do Sul and in the Santa Catarina Island, with exception of *O. flavescens*. However, this species may be taken as a habitat generalist and is normally found in a variety of habitats in southern Brazil. On the other hand, the taxonomical status of the small *Oryzomys* species (subgenus *Oligoryzomys*) is poorly understood and the relationships of several populations must be reviewed.

The southern and central rodent assemblages of the Coastal Plain present high similarity with the Uruguayan and eastern Argentina fauna (compare SANBORN, 1929; CABRERA, 1961; MASSOIA, 1961, 1964; XIMENEZ et al., 1972; MARCONI and KRAVETZ, 1986) and resemble more to the Pampean Province (FITTKAU. 1969; CABRERA and WILLINK, 1973) and to the Uruguayan centre of MÜLLER (1973) which extends its range from south Brazil and Uruguay to eastern Argentina. In the south of the Coastal Plain the grasslands and swamps are actually dominant. The open and semiarborized landscapes were documented to the Late Pleistocene (SOLIANI, 1973; PAULA COUTO, 1975) and palynological evidences suggest that grasslands and swamps are old formation in this region occurring at least from the beginning of the Early Würm (LORSCHEITER and ROMERO, 1985).

None of the cricetid species found is typical of the Restinga, since all of them occur in neighbouring areas and several are largely distributed in other regions of South America. This is in close agreement with the flora that is largely composed by tropical and subtropical

elements derived from neighboring areas (RAMBO, 1954; SMITH, 1962; WAECHTER, 1985).

The rodent distribution pattern along the north-south gradient contrasts with the occurrence of the sand lizard *Liolaemus occipitalis* (SAURIA, IGUANIDAE) that inhabits the Restinga from Uruguay to the North of the Santa Catarina Island (MÜLLER, 1975). The three allopatrically dispersed sand lizards of the genus *Liolaemus* in south/southeast Brazil (*L. occipitalis*, *L. wiegmannii*, *L. lutzae*) showed that southern faunal elements have expanded their distribution towards the north along the coastal dunes corridors (VANZOLINI and AB'SABER, 1968; MÜLLER, 1970, 1973, 1975, 1981). In several periods of lower sea-level during the Quaternary (LORSCHEITTER and ROMERO, 1985; MARTIN et al, 1986a, 1986b), a continuous strip of sand ridges can be shown to have existed connecting southern and eastern regions of the brazilian coast. At least in the south (MÜLLER, 1970, 1973) this continuous strip of Restinga must have acted as a migration corridor for southern elements. Nevertheless, the factors that largely determine the cricetid rodent assemblages' features differ from those that determinate the occurrence of other groups more related to the almost vegetation-free drifting sand dune habitats. The cricetid rodent assemblages' characteristics are largely determined by the habitat features. They are affected mainly by patch structure and dynamics of sites with hig relative importance of vegetation. Environmental variables as those related to the habitat structure (e.g. ground cover, foliage height density) are known to limit their occurrence. Normally the cricetid species avoid the drifting sand dunes, completely devoid of vegetation. Likewise, sand dunes, where foliage cover and density are low, are not suitable habitats for the majority of the

species. Only *C. laucha* was observed in almost naked dunes near the coast. The ability to use burrows as shelters and nests, facilitates the survival of this species in more extreme habitats. Other species as *O. flavescens* and *D. kempi* were found in coastal dunes but in close association to sites with high cover of *A. trigynum* (CYPERACEAE).

The treeless habitat types compose almost a continuum from Uruguay to Santa Catarina, contrasting with the more complex region in the west side of the coastal strip, whose landscape is formed by a mosaic of patchs of forests, swamps, and wet and dry grasslands. It seemed likely that the dynamics of the drifting sand dunes region did not have affected significantly the characteristics of the cricetid rodent fauna along the coast of southern Brazil. Such pattern contrasts to other groups as the caviomorph fossorial rodents *Ctenomys* (CTENOMYIDAE) (TRAVI, 1981; FREITAS, 1987, 1990) or sand lizards *Liolaemus* (MÜLLER, 1970; MÜLLER and STEINIGER, 1977) that are more related to sandy open lansdcapes. Thus some grassland or coastal dune Restinga rodent species as *Ctenomys torquatus*, *C. flamarioni* and *C. minutus* are more related to the recent geological evolution of the Coastal Plain (FREITAS and LESSA, 1984; FREITAS, 1990). The latter two species are typical from south brazilian Restinga. Such endemisms as the caviomorph rodents (genus *Ctenomys* and possible *Cavia* - *Cavia magna* (CAVIIDAE) (XIMENEZ, 1980)), and the sand lizards of the genus *Liolaemus* desagree with the pattern of the phanerogamous flora analysed by RAMBO (1954). He concluded that the entire phanerogamous flora of the Restinga is imigrated from the neighbouring areas and presents no endemic species. Likewise, the Restinga cricetid rodent fauna constitutes a subset of the neighbouring areas and is more related to

the history of the vegetation like the coastal forest belts, and extensive grasslands or swamps. However, the within-assemblages peculiarities, concerning their structure and composition, are partially determined by the geological features that primarily delimit several terraces over which the mosaic of habitats occurs.

The Restinga in southern Brazil constitutes a complex of formations, ranging from almost naked dunes, grasslands, grassy swamps, to shrubby and dense forests. Several vegetation zones contrast strongly, and the drain conditions may play a central role in different habitat types. The geomorphology is certainly the basic reason for occurring such differences since the vegetation zones are partially conditioned by the complex system of sandy and lagoonal terraces that extend along the coast.

In a general manner, the cricetid fauna studied in the Restinga and adjacent areas is related to the main habitats and some microhabitat structural variables, summarized as follows:

Species/ Sampled areas	Habitats	Microhabitat structural variables
TAIM		
O. rufus	dry grasslands	+FHD50
D. kempi	wet grasslands and ecotones	+FHD170/+HHT
A. azarae	shrublands and dry grasslands	-TDIS/-MUD
A. serrensis	all habitats mainly forests and shrublands	+TDIS/+TDIA
S. tumidus	ecotones	+FLOOD/+HHT

-Continued.

Species/ Sampled areas	Habitats	Microhabitat structural variables
TAIM		
O. flavescens	mainly grasslands	+HCV/-TDIS
O. delticola	forests/ecotones	+CANCV/-FHD170
H. brasiliensis	swamps/grasslands	.
C. laucha	pastures/sand dunes	.
CAPAO DO LEAO		
S. tumidus	corridors	+FLOOD/+FHD25
O. flavescens	grasslands	+FHD25/+HCV
O. delticola	forests/ecotones	+TDIS/-FLOOD
O. ratticeps	swamp forests	+ROHIHO/+TDIA
H. brasiliensis	ecotones	+FLOOD/+FHD100
FAXINAL		
A. cursor	forests/shrublands	.
A. nigrita	shrublands	+HCV/+FLOG
B. lasiurus	butiá savana	.
O. iheringi	forests/shrublands	+TDIS/+TDIA
O. ratticeps	forests/thickets	-FHD170/-HCV
O. nigripes	shrublands	+HCV/+FLOG
COSTA DE DENTRO		
O. hispidus	shrublands/woodlands	+FHD170/-TDIA
A. cursor	forests/shrublands	.
N. squamipes	stream edges	+FLOOD
O. nitidus	swamp forests	+FHD170
O. ratticeps	forests	-FHD170/+ROCAV
O. flavescens	grassy swamps	.
O. nigripes	forests	+FHD170

The signs (+-) denote the trends of the rodent environmental variable relationships. The acronyms are from Tab. 1.

Such habitats are characterized by a complex of variables. Several of them affected the species observed in this study and contributed to explain the major trends among the recognized gradients. However, when taked separately, many of them seemed to be less satisfactory as predictors and were difficult to be related to the species occurrence mainly due to the structural habitat complexity and the ultimate and proximate effects on the rodent abundance. The distribution of many species was clearly related to differences in habitat structure suggesting that the overlapping occurrence and certainly the species richness are largely related to the existence of several vegetational types. Thus the gradient models that invoke a continuous habitat distribution by using environmental variable sets seem more satisfactory since some species are more related to the macrohabitat than to the microhabitat structural variations.

The univariate analysis relating the number of rodent species to various environmental variables fail to find significant correlations in some of the regions studied. Only in the south of the Coastal Plain significant correlations were observed. In the Taim region the number of species caught were related to the herb layer features (foliage height density and herbaceous height). In the Capao do Leao region the only variable related significantly to the species number was the relative importance of muddy sites. This last variable has no defined relation to the species but shows that the sites on the low lagoonal terrace tend to sustain a more diverse rodent assemblage. In the northern, the more tropical regions (Faxinal and Costa de Dentro - Santa Catarina Island), no significant correlation was observed between the species number by habitat and the mean of the environmental variables. Such pattern can be interpreted

in a causal way and may be related to the landscape features. The mosaic of habitats analysed is composed mainly by a complex of zonations and vegetational successions. Several seral stages are derived from an original matrix that probably was not originally so differentiated.

In Faxinal no significant correlation was observed between the number of captures and the environmental variables. In this region the extensive areas composed mainly of arborescent shrubs (*Baccharis sp.*) and by dense herbaceous layer are not restrictive for the rodent assemblage as a whole. Such apparently persistent secondary growth formations, despite the structural differences if compared to the forests sites, present normally high density of rodents.

In Costa de Dentro (Santa Catarina Island) the forests appear to be the most suitable habitats for the cricetid fauna. The number of captures in this region was significantly correlated to a large set of variables that are associated to forest sites or to the hill slopes. The open habitats or those departing from the forest features are less appropriate for the rodent community.

In both the above mentioned regions, the differences between the captures when relating to the trap sites, could not be explained by the full environmental variables set. The partial Canonical Correspondence Analysis normally failled to find significant relations between the rodents and the microhabitat structure. This may be at least partly due to the gradual variations among the sites. Some of them, despite structural differences, were originated from the same original matrix and present several common features resulting thus in a low species turnover between the habitat types. The rodent fauna of such habitats (even if seral stages or related to the

natural zonations) represents a subset of species that occur in the tropical forest, the original main formation. In the southern regions the species turnover is notable. The grasslands present a partially distinct small mammal composition, compared to the forests. The open formations are dominant and some grassland species live alongside forest elements.

In Taim, the southernmost region studied, no variables were significantly correlated to the number of captures. Even though distinct in composition, the rodent assemblage used all the available habitats. In Capão do Leão the significant correlation obtained between the number of captures and two of the variables related to forest structure (canopy cover and tree spatial disposition) may be taken as an evidence for habitat disturbance. Some species (*H. brasiliensis*, *S. tumidus*, and *O. flavescens*) that may potentially occur with high density in grassy sites were limited to forest edges or to some patchy areas in the grassland. The numerically dominant species (*O. delticola*) was more related to wooded sites. The livestock grazing limits the grassland species. The higher density of rodents occurs inside the forests, in forest edges and in those habitats that depart from grassland features.

Along the Restinga in Rio Grande do Sul, particularly in the southern and central portions, where extensive "grazing lawns" occur, rodents are virtually lacking. In such areas the species are distributed in patches and their occurrence is largely limited by the microhabitat availability. The habitat colonization rate, and the extinction of populations, play certainly the main role in determining the structure of the assemblages in such patchy habitats. In areas where open vegetation as grasslands predominates in the landscape, the population size and the community richness are strongly lowered by

habitat disruption. Consequently, grassland species are restricted to forest or swamp edges. Only in sites virtually free of the livestock grazing effects the rodent assemblages approximate to the original composition.

Theoretical and empirical foundations of community ecology suggest that the species assemblage patterns are determined by the availability of limiting resources (MacARTHUR, 1972; SHOENER, 1974; GRANT, 1986; ROUGHGARDEN, 1986) and by competition (LEVINS, 1968; MacARTHUR, 1972; GRANT, 1972; PIANKA, 1974; HUTCHINSON, 1975; FRAMSTAD and STENSETH, 1984; BROWN et al., 1986). The habitat is a complex resource and its availability and structure play an important role in the community organization, particularly for small rodents (ROSENZWEIG and WINAKUR,1969; M'CLOSKEY, 1976; DUESER and SHUGART, 1978, 1979; HALLET, 1982; ROSENZWEIG et al., 1984). However, the relative independent effect of competition and habitat structure on habitat use is complex and has been studied in several rodent assemblages mainly by multiple-regression approaches (ABRAMSKY, 1981; HALLET et al., 1983; ROSENZWEIG et al., 1984; DUESER and PORTER, 1986; LACHER and ALHO, 1989). Such non-destructive techniques, despite the use with concern by some authors (ABRAMSKY et al., 1986; ROSENZWEIG et al., 1985), have a great advantage on manipulative experiments (PIMM, 1985; LACHER and ALHO, 1989). The interaction coefficients may be normally near zero due to the fact that the ecological scale is not appropriate for discerning competition (MacARTHUR, 1972). On the other hand, the actual pattern on habitat use among species may have evolved as a result of past competition (ROSENZWEIG, 1974, 1977; PIMM and ROSENZWEIG, 1981), or by specific habitat requirements (FRAMSTAD and STENSETH, 1984). By this way, the species

interactions may be very weak or not detectable at present.

The results obtained in southern Restinga lend strong support to the hypothesis that the microhabitat structure determines the rodent assemblage features. In this region, the centers of abundance of each species are normally in different plant associations or in recognized sites in the same formation. Some species were associated primarily with herbaceous vegetation and some with woody. The observed differences among the species captures could be explained by the environmental variables. A subset as those that characterize the herb layer (herbaceous cover and foliage height density) normally explain very well the rodent distribution. Where data were available to test the significance of the species interactions, as in the Taim region, except for one pair of species (*A serrensis* and *O. delticola*), all the partial regression coefficients were not significant. In this way, the hypothesis that interespecific competition molds pattern of habitat used by such assemblage has no support. This indicates that mutual inhibitory relationships between species may not be common. Furthermore, the habitat structure has the greatest effect on the species distribution, compared to the species interactions. The results show that the prediction of the assemblage composition and structure, within a single biogeographic unit, and in relatively small areas, can be made by the habitat features since the faunal changes normally accompany changes in the habitat structure and structurally similar habitats are inhabited by similar assemblages. Therefore, the habitat selection appears to be the major factor to sort species among the habitats. In this way, the microhabitat availability controls the number of species.

The Restinga rodents species are normally segregated by the habitats in a spatial scale. In the southern regions, coarse-grained habitats lead to a great species turnover (β diversity). The strong habitat association among the species in areas where the vegetation changes drastically along the drainage lowlands, or associated to sandy terraces, suggests that the habitat pattern use is the product of a previous coevolution in a similar complex landscape. In northern regions, the more fine-grained habitats, despite the structural differences, lead to a more homogeneous species distribution among the habitats and consequently to a low species turnover between the vegetation zones. The species in these regions occur also in secondary formations, that are derived from the original lowland tropical forest.

The apparent resistence of Restinga rodent communities to invasion by *Rattus* and *Mus* suggests that the habitats are species saturated, even if saturations differ among the habitat types. *M. musculus* and *R. rattus* have successfully colonized a wide variety of habitats throughout the world and are usually more associated with commensal and disturbed situations (BRONSON, 1979; NOWAK and PARADISO, 1983), and exploit otherwise depauperated small mammal habitats (BERRY and TRICHER, 1969; NEWSOME, 1969; BRAITHWAITE et al., 1978; FOX, 1982,1985). *M. musculus* was found in relatively simpler habitats near the coast together with *D. kempi* and *O. flavescens*. *R. rattus* was trapped only once in the Pontal de Tapes; a peninsula in the Patos Lagoon. The occurrence of this species may be affected more by interaction with other species than by the habitat structure. The murids appear to be weak competitors and in complet assemblages the species certainly do not occur. Some coastal areas present a depauperated rodent fauna and appear to be more extreme

habitats to several species. In this way, unsaturated habitats appear to occur near the Atlantic coast and peninsulas (and certainly in islands) of the Patos Lagoon. Certainly, events as colonization and species extinction play an important role in the structure and composition of the rodent assemblages in the patchy and structurally simple habitats on the extensive sandy areas along the Restinga.

V. CONCLUSIONS

The evaluation performed in seventeen areas along the Coastal Plain, and in the south-brazilian highland slopes in Rio Grande do Sul and in the Santa Catarina Island, demonstrated that the rodent fauna is differently composed particularly along the coasts. The assemblages composition varies markedly from North to South and West to East as a result of a complex interplay of historical and ecological factors. The north-south gradient represents mainly the interface between tropical and subtropical regions since the composite fauna reflects major continental patterns. The west-east gradient is closely related to local ecological conditions, partially determined by the geological history of the Coastal Plain.

None of the rodent species found, is typical to the Restinga and several elements which are largely distributed in South America. The assemblages from the northern regions of the coast showed high similarity to those found in the south-brazilian highland slopes. This fact is in close agreement with the flora pattern that is composed mainly by tropical forest elements derived from neighbouring areas. The southern and central assemblages are composed for the most part by sub-tropical elements more related to the open landscapes of Uruguay and eastern Argentina. Some northern forest species occur in southern regions showing that Restinga forests along the coast acted as corridors for some tropical elements. In northern regions, despite the structural differences among the habitats, there is a low species turnover between the vegetation zones. Several species occur also in secondary formations that are derived mainly from the original

lowland tropical forest. In the southern regions, the species turnover is greater partly due to the fact that grassland species tend to live alongside forest elements.

Across the range of regions studied, the results indicate that the main reason for changes in the rodent assemblage characteristics is the availability of suitable habitats and the microhabitat features. The correlation and ordination analysis of rodent and/or species numbers in relation to various environmental factors disclosed several relationships which can be interpreted in a causal way. The major habitat availability functions as an ultimate factor and the suitable physical structure of the microhabitats as a proximate one. Environmental variables such as those related to the microhabitat structure (e.g. ground cover, foliage height density) are known to limit the species occurrence. Normally the rodent species reacted to sudden differences in the microhabitat structures. When the analysis fails to find significant relations between the species and the microhabitat features, the major habitat characteristics appear to explain the species distribution and trends along the gradients.

The cricetid rodent assemblages' peculiarities are largely determined by the habitat features and are affected mainly by patch structure and dynamics of sites with high relative importance of vegetation in the west side of the coastal strip whose landscape is formed by a mosaic of forests, swamps and grasslands. Thus the dynamics of the drifting sand dunes have not affected significantly the characteristics of the cricetid rodent fauna along the coast of southern Brazil since such regions normally do not present suitable habitats for the majority of the species.

The results show that the prediction of the assemblages composition and structure, within a single biogeographic unit, and in relatively small areas, can be made by the habitat features since the faunal changes normally accompany changes in the habitat structure and structurally similar habitats are inhabited by similar assemblages.

The virtual absence of significant interactions between the species in one assemblage analysed in southern Restinga lend strongly support the hypothesis that the microhabitat structure alone determines the rodent assemblage features, and that the habitat selection appears to be the major factor in distributing the species among the habitats. Mutual inhibitory relationships between species are not common and the effects of other species on the distribution and abundance of a species appear to be relatively less important than the effects of habitat structure.

The strong habitat association related to the absence of significant interactions among the species in areas where the vegetation changes drastically in a spatial scale suggests that the habitat pattern use is the product of a previous co-evolution of the assemblage in a similar complex landscape. Beside the influence of competition in the past, that may have affected the actual pattern of the assemblage, the diversity of forms and the strong association of species with some components of the landscape suggest that the pattern of habitat and microhabitat use may have evolved by specific habitat requirements. Thus the landscape composition, the availability of habitats and the microhabitat features appear to be the primary factors that mold the rodent assemblages composition and structure in the south brazilian Restinga.

Die Restinga-Regionen Südbrasiliens sind im Hinblick auf alle Standortfaktoren sehr verschiedenartig. Vegetationslose Dünen, grassbedeckte Sümpfe, offene Waldtypen und geschlossene Wälder wechseln einander ab. Für die Verbreitung dieser Vegetationsmosaike haben die Wasserhaushaltsbedingungen eine zentrale Bedeutung.

In vorliegender Arbeit wurde die Rodentia-Fauna 17 verschiedener Gebiete untersucht, die entlang der Küstenebene, den südbrasilianischen Randgebirgsabdachungen und auf der Insel Santa Catarina liegen.

Die Spezieszusammensetzung zeigt deutliche Unterschiede zwischen Norden und Süden bzw. Westen und Osten. Die Nagetier-Gemeinschaften im nördlichen Teil der Küste von Rio Grande do Sul und auf der Insel Santa Catarina besitzen große Gemeinsamkeiten mit denen, die an den südbrasilianischen Hochlandböschungen gefunden wurden. Insofern korrelieren die Veränderungen in der Artenzusammensetzung nicht mit den abrupten Veränderungen topographischer Merkmale.

Die nördlichen Restinga-Gemeinschaften besitzen mehr Arten des tropischen Waldes. In den zentralen und südlichen Nagetiergemeinschaften überwiegen im Gegensatz dazu die Gemeinsamkeiten mit der Fauna Uruguays und der östlichen Argentiniens. Einige Spezies sind sogar an Grasslandschaften gebunden.

Keine der gefundenen Cricetidae-Arten kommt ausschließlich in der Restinga vor. Alle sind auch in Nachbargebieten verbreitet. Das Areal einiger Arten reicht über weite Teile Südamerikas hinaus.

In 4 Untersuchungsgebieten basierte die Verteilung der Fangplätze auf "sample scores", um das Verhältnis zwischen Spezies und Habitat besser einschätzen zu können. Die Bedeutung, des Einflusses der Habitatstruktur auf die Nagetierverteilung wurde durch Kanonische Korrespondenzanalyse ermittelt, und die Signifikanz der Ordination mit Hilfe des "Monte Carlo Permutations-Tests" geprüft. Dabei zeigte inh, daß die Artenzusammensetzung hauptsächlich durch die Habitatmerkmale bestimmt wird.

In einem Untersuchungsgebiet wurde "Multiple Regressionsanalyse" angewendet, um festzustellen, inwieweit die Verbreitung des Vorkommen der Arten von der Habitatstruktur bzw. von den Speziesinteraktionen abhängt. Dabei wurde eine Gemeinschaftsmatrix erstellt, die den Speziesinteraktions-koeffizienten zwischen den Artenpaaren darstellt. Die Ergebnisse bestätigen die Hypothese, daß die Mikrohabitatstruktur die Nagetiergemeinschaften bestimmt, und daß die gegenseitige Hemmung zwischen den Spezies geringere Bedeutung besitzt. Durch die Habitatmerkmale, innerhalb derselben geographischen Einheit oder eines relativ kleinen Gebietes, können Voraussagen für die Gemeinschaftszusammensetzung und -struktur gemacht werden. Die Veränderungen in der Gemeinschaftszusammensetzung werden gewöhnlich von Veränderungen in der Habitatstruktur begleitet. Nach unseren Untersuchungen ist die aktive Habitatwahl der wichtigste Faktor für die Verbreitung der verschiedenen Arten.

RESUMO

As formações de Restinga no Sul do Brasil são compostas por vários complexos vegetacionais. As zonas variam desde dunas completamente desprovidas de vegetação, a campos secos, campos alagáveis, banhados e florestas. As características de vários tipos de hábitats são largamente influenciadas pelas condições de drenagem da região.

Avaliações em 17 áreas ao longo da costa do Rio Grande do Sul, Ilha de Santa Catarina e encosta do Planalto Sul-Brasileiro demonstram que a composição da fauna de roedores varia marcadamente no sentido Norte-Sul. As congregações de espécies do extremo Norte da costa do Rio Grande do Sul (Faxinal - Torres) e da Ilha de Santa Catarina (Costa de Dentro) são muito similares às da encosta do Planalto onde a Mata Atlântica é a formação dominante. A fauna das regiões mais ao Sul é mais similar à do Uruguai e Leste da Argentina onde predominam as formações abertas. Desta forma, as congregações de espécies mudam as suas características em concordância com as zonas dominantes de vegetação.

Em quatro regiões, as estações de captura, quando positivas, foram descritas quanto às suas características estruturais e submetidas à Análise Canônica de Correspondência (CCA) com o objetivo de avaliar as relações entre as espécies de roedores e a estrutura dos hábitats. A avaliação do efeito de subconjuntos de componentes estruturais dos hábitats foi efetuada através da análise parcial Canônica de Correspondência. O significado das ordenações foi avaliado através de um teste de permutações (Monte Carlo) gerando associações

aleatórias entre roedores e variáveis. Para uma área amostrada no Sul da Planície Costeira do Rio Grande do Sul (Estação Ecológica do Taim) foram estimados independentemente os efeitos relativos da estrutura dos hábitats e das interações interespecíficas na distribuiçao das espécies. Os resultados evidenciam que a estrutura dos hábitats é o maior fator condicionador da distribuição dos roedores e que as interações interespecíficas não são importantes. Desta forma, a predição da composição e estrutura das assembléias de roedores, dentro de uma mesma unidade biogeográfica, pode ser efetuada com base nas características estruturais dos hábitats. A seleção dos mesmos é o principal mecanismo pelo qual as espécies repartem o espaço.

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APPENDIX

APPENDIX 1. Euclidean distance (d_{jk}) between the sampled areas based upon rodent taxonomic composition. $\overline{d_{jk}}$ = 2.50; s = 0.71; r_{cd} = 0.790. 1. Costa de Dentro (Santa Catarina Island), 2.Faxinal, 3. Alto Ferrabraz (Sapiranga), 4. Picada Verão (Sapiranga), 5. Morro Alto (Osório), 6. Pontal Palmital (Osório), 7. Morro Osório (Osório), 8. Osório (southeast town), 9. Emboaba (Osório, east Emboaba Lake), 10. Imbé (Tramandaí), 11. Lenha Seca (Osório - west Tramandaí Lagoon), 12. Saco Mole (north Tramandaí Lagoon), 13. Delta Tramandaí (Tramandaí), 14. Pontal de Tapes (Tapes), 15. Capão do Leão (Mostardas), 16. Banhado do Alemão (Pelotas), 17. Taim Ecological Reserve (Rio Grande/Santa Vitória).

	1	2	3	4	5	6	7	8	9	10	11
1											
2	2.65										
3	2.65	2.45									
4	2.45	2.23	1.73								
5	2.00	1.73	2.65	2.83							
6	1.73	2.00	2.45	2.65	1.00						
7	2.23	1.41	2.83	2.23	1.73	2.00					
8	2.64	2.00	2.82	2.64	1.73	2.00	2.00				
9	2.44	2.24	3.00	3.16	1.41	1.73	2.24	1.73			
10	2.82	3.00	3.00	3.16	2.45	2.24	3.00	2.24	2.00		
11	2.64	2.45	3.16	3.31	1.73	2.00	2.45	2.00	1.00	1.73	
12	2.82	3.00	3.00	3.16	2.45	2.24	3.00	2.24	2.00	0.00	1.73
13	2.82	3.00	3.00	3.16	2.45	2.24	3.00	2.24	2.00	0.00	1.73
14	3.16	3.00	3.31	3.46	2.45	2.65	3.00	2.65	2.45	2.00	2.24
15	2.82	3.00	3.31	3.46	2.45	2.24	3.00	2.65	2.45	2.00	2.24
16	3.31	3.46	3.46	3.60	3.00	2.83	3.46	2.83	3.00	2.24	2.83
17	3.74	3.87	3.87	4.00	3.46	3.32	3.87	3.32	3.16	2.45	3.00

APPENDIX 1. (cont.)

	12	13	14	15	16
12					
13	0.00				
14	2.00	2.00			
15	2.00	2.00	2.45		
16	2.24	2.24	2.65	1.73	
17	2.45	2.45	2.45	2.45	1.73

APPENDIX 2. Taim region. Simple correlation coefficient (r) relating environmental variables measured at each trap site. The variable acronyms are from Table 1.

	HHT	HCV	FHD25	FHD50	FHD100	FH170	CANHT
HHT							
HCV	0.413						
FHD25	0.489	0.746					
FHD50	0.603	0.742	0.923				
FHD100	0.757	0.672	0.741	0.904			
FHD170	0.834	0.520	0.552	0.725	0.920		
CANHT	-0.102	-0.615	-0.649	-0.595	-0.460	-0.272	
CANCV	-0.412	-0.806	-0.751	-0.724	-0.617	-0.457	0.769
TDIA	-0.019	-0.506	-0.492	-0.470	-0.360	-0.202	0.813
TDIS	-0.060	-0.643	-0.520	-0.527	-0.438	-0.279	0.702
BRANCH	-0.114	-0.608	-0.628	-0.580	-0.438	-0.266	0.832
FLOG	-0.116	-0.421	-0.425	-0.371	-0.280	-0.137	0.330
SHRUB	-0.022	-0.421	-0.266	-0.240	-0.178	-0.122	0.145
ROHIHO	-0.332	-0.650	-0.594	-0.588	-0.532	-0.435	0.572
LIT	0.231	0.408	0.241	0.240	0.223	0.296	-0.068
MUD	0.207	-0.460	-0.312	-0.247	-0.135	-0.032	0.372
FLOOD	0.259	-0.161	-0.110	-0.110	-0.063	0.033	0.339

n = 63; significance level $P_{0.05} = 0.250$; $P_{0.01} = 0.325$; $P_{0.001} = 0.408$.

APPENDIX 2 (cont.).

	CANCV	TDIA	TDIS	BRANCH	FLOG	SHRUB	ROHIHO
CANCV							
TDIA	0.577						
TDIS	0.641	0.442					
BRANCH	0.738	0.680	0.732				
FLOG	0.420	0.211	0.308	0.277			
SHRUB	0.290	0.081	0.387	0.224	0.243		
ROHIHO	0.589	0.363	0.535	0.461	0.358	0.230	
LIT	-0.346	0.047	-0.244	-0.075	-0.125	-0.340	-0.353
MUD	0.340	0.329	0.439	0.335	0.186	0.460	0.237
FLOOD	0.129	0.272	0.277	0.261	0.217	0.110	0.389

n = 63; significance level $P_{0.05}$ = 0.250; $P_{0.01}$ = 0.325; $P_{0.001}$ = 0.408.

APPENDIX 2 (cont.).

	LIT	MUD
LIT		
MUD	-0.321	
FLOOD	0.061	0.394

n = 63; significance level $P_{0.05}$ = 0.250; $P_{0.01}$ = 0.325; $P_{0.001}$ = 0.408.

APPENDIX 3. Capão do Leão region. Simple correlation coefficient (r) relating environmental variables measured at each trap site. The variable acronyms are from Table 1.

	HHT	HCV	FHD25	FHD50	FHD100	FH170	CANHT
HHT							
HCV	0.327						
FHD25	-0.052	0.613					
FHD50	0.064	0.634	0.950				
FHD100	0.140	0.613	0.779	0.903			
FHD170	0.055	0.643	0.695	0.792	0.933		
CANHT	0.063	-0.353	-0.269	-0.260	-0.259	-0.357	
CANCV	-0.165	-0.808	-0.656	-0.635	-0.559	-0.596	0.435
TDIA	0.171	0.013	-0.065	-0.055	-0.020	-0.080	0.652
TDIS	-0.093	-0.616	-0.476	-0.500	-0.454	-0.428	0.250
BRANCH	0.048	-0.338	-0.357	-0.348	-0.287	-0.304	0.631
FLOG	-0.159	-0.452	-0.349	-0.439	-0.481	-0.506	0.350
SHRUB	-0.020	-0.349	-0.481	-0.447	-0.325	-0.220	0.073
ROHIHO	-0.054	-0.426	-0.451	-0.509	-0.509	-0.503	0.453
LIT	-0.063	-0.178	-0.115	-0.174	-0.203	-0.245	0.494
MUD	0.381	0.107	-0.053	0.012	0.098	0.128	-0.178
FLOOD	0.264	0.321	0.368	0.443	0.424	0.343	-0.326

n = 41 ; significance level $P_{0.05}$ = 0.304; $P_{0.01}$ = 0.393; $P_{0.001}$ = 0.490.

APPENDIX 3 (cont.).

	CANCV	TDIA	TDIS	BRANCH	FLOG	SHRUB	ROHIHO
CANCV							
TDIA	-0.051						
TDIS	0.733	-0.136					
BRANCH	0.560	0.257	0.305				
FLOG	0.523	0.117	0.388	0.289			
SHRUB	0.628	-0.308	0.690	0.351	0.295		
ROHIHO	0.545	0.392	0.442	0.373	0.447	0.170	
LIT	0.220	0.214	0.064	0.330	0.141	-0.059	0.168
MUD	-0.057	-0.231	0.099	-0.049	-0.137	0.404	-0.289
FLOOD	-0.286	-0.177	-0.125	-0.296	-0.120	0.145	-0.323

n = 41 ; significance level $P_{0.05}$ = 0.304; $P_{0.01}$ = 0.393; $P_{0.001}$ = 0.490.

APPENDIX 3 (cont.).

	LIT	MUD
LIT		
MUD	-0.361	
FLOOD	-0.477	0.474

n = 41 ; significance level $P_{0.05}$ = 0.304; $P_{0.01}$ = 0.393; $P_{0.001}$ = 0.490.

APPENDIX 4. Faxinal region. Simple correlation coefficient (r) relating environmental variables measured at each trap site. The variable acronyms are from Table 1.

	HHT	HCV	FHD25	FHD50	FHD100	FH170	CANHT
HHT							
HCV	0.765						
FHD25	-0.098	0.144					
FHD50	0.190	0.425	0.887				
FHD100	0.513	0.741	0.617	0.830			
FHD170	0.549	0.726	0.514	0.685	0.907		
CANHT	-0.576	-0.783	-0.230	-0.455	0.687	-0.671	
CANCV	-0.762	-0.872	-0.114	-0.372	-0.661	-0.623	0.794
TDIA	-0.476	-0.529	-0.206	-0.312	-0.498	-0.462	0.728
TDIS	-0.363	-0.708	-0.240	-0.340	-0.583	-0.629	0.771
BRANCH	-0.464	-0.645	-0.101	-0.315	-0.521	-0.527	0.854
FLOG	0.232	0.083	0.148	0.170	0.181	0.209	0.049
SHRUB	-0.483	-0.448	-0.066	-0.284	-0.383	-0.371	0.277
ROHIHO	-0.420	-0.665	-0.201	-0.281	-0.485	-0.472	0.601
LIT	-0.272	0.090	0.438	0.322	0.230	0.225	-0.261
MUD	-0.375	-0.396	-0.067	-0.174	-0.343	-0.364	0.579
FLOOD	0.091	-0.359	-0.216	-0.202	-0.316	-0.335	0.386

n = 57 ; significance level $P_{0.05}$ = 0.273; $P_{0.01}$ = 0.354; $P_{0.001}$ = 0.443.

APPENDIX 4 (cont.).

	CANCV	TDIA	TDIS	BRANCH	FLOG	SHRUB	ROHIHO
CANCV							
TDIA	0.511						
TDIS	0.717	0.671					
BRANCH	0.688	0.626	0.716				
FLOG	-0.127	0.181	0.014	0.142			
SHRUB	0.487	0.102	0.097	0.145	-0.124		
ROHIHO	0.545	0.597	0.651	0.425	0.197	0.249	
LIT	-0.081	-0.223	-0.287	-0.310	-0.178	0.017	-0.254
MUD	0.532	0.283	0.384	0.555	0.010	0.256	0.186
FLOOD	0.233	0.410	0.515	0.324	0.289	0.087	0.511

n = 57 ; significance level $P_{0.05}$ = 0.273; $P_{0.01}$ = 0.354; $P_{0.001}$ = 0.443.

APPENDIX 4 (cont.).

	LIT	MUD
LIT		
MUD	-0.284	
FLOOD	-0.530	0.182

n = 57 ; significance level $P_{0.05}$ = 0.273; $P_{0.01}$ = 0.354; $P_{0.001}$ = 0.443.

APPENDIX 5. Costa de Dentro region. Simple correlation coefficient (r) relating environmental variables measured at each trap site. The variable acronyms are from Table 1.

	HHT	HCV	FHD25	FHD50	FHD100	FH170	CANHT
HHT							
HCV	0.149						
FHD25	-0.241	0.160					
FHD50	-0.146	0.347	0.790				
FHD100	0.106	0.558	0.376	0.731			
FHD170	0.332	0.543	0.057	0.304	0.734		
CANHT	-0.150	-0.439	-0.146	-0.274	-0.234	-0.298	
CANCV	-0.040	-0.675	-0.316	-0.490	-0.488	-0.381	0.713
TDIA	0.049	-0.189	-0.162	-0.224	-0.204	-0.272	0.505
TDIS	-0.031	-0.448	-0.340	-0.517	-0.475	-0.378	0.555
BRANCH	-0.129	-0.419	-0.100	-0.203	-0.290	-0.304	0.302
FLOG	-0.071	-0.201	0.023	-0.026	-0.015	-0.183	0.363
SHRUB	-0.243	-0.145	0.302	0.293	-0.042	-0.174	-0.339
ROHIHO	0.137	0.094	-0.271	-0.272	-0.109	0.283	0.098
LIT	-0.059	-0.365	-0.138	-0.278	-0.177	0.046	0.393
MUD	-0.084	0.130	0.181	0.068	-0.101	-0.190	0.004
FLOOD	-0.029	0.152	0.294	0.125	-0.033	-0.112	-0.029
ROCK	-0.085	-0.498	0.064	0.075	-0.097	-0.395	0.336
ROCAV	-0.139	-0.305	0.113	0.032	-0.144	-0.359	0.603
SLOPE	-0.317	-0.642	0.126	0.025	-0.282	-0.591	0.421

n = 49 ; significance level $P_{0.05}$ = 0.287; $P_{0.01}$ = 0.372; $P_{0.001}$ = 0.465.

APPENDIX 5 (cont.).

	CANCV	TDIA	TDIS	BRANCH	FLOG	SHRUB	ROHIHO
CANCV							
TDIA	0.181						
TDIS	0.636	0.314					
BRANCH	0.532	0.103	0.406				
FLOG	0.493	0.097	0.143	0.225			
SHRUB	-0.050	-0.488	-0.294	-0.062	0.029		
ROHIHO	0.229	0.004	0.260	0.264	-0.086	-0.315	
LIT	0.554	-0.076	0.433	0.298	0.066	-0.077	0.341
MUD	-0.176	0.160	-0.100	-0.116	-0.131	-0.103	-0.065
FLOOD	-0.194	0.087	-0.137	-0.084	-0.074	-0.047	-0.067
ROCK	0.359	0.077	0.067	0.273	0.274	0.121	-0.340
ROCAV	0.457	0.124	0.228	0.309	0.334	-0.025	-0.141
SLOPE	0.525	0.039	0.248	0.440	0.398	0.362	-0.328

n = 49 ; significance level $P_{0.05}$ = 0.287; $P_{0.01}$ = 0.372; $P_{0.001}$ = 0.465.

APPENDIX 5 (cont.).

	LIT	MUD	FLOOD	ROCK	ROCAV
LIT					
MUD	-0.228				
FLOOD	-0.174	0.569			
ROCK	0.139	-0.170	-0.097		
ROCAV	0.314	-0.105	-0.060	0.549	
SLOPE	0.292	-0.191	-0.109	0.729	0.686

n = 49 ; significance level $P_{0.05}$ = 0.287; $P_{0.01}$ = 0.372; $P_{0.001}$ = 0.465.

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